Function of nest construction in relation to foraging behaviour of cribellate web spiders (Eresidae) and wandering spiders (Heteropodidae) of the Namib and Negev Deserts

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General Aim of Project: To examine the comparative nest structures of ground-living web spiders, Eresidae, and burrow-living wandering spiders, Heteropodidae, of the Namib and Negev Deserts in relation to their respective foraging, thermoregulation and anti-predator requirements and environment.

1. Introduction

Seothyra Nests: A horizontal flat closely woven web beneath a thin layer of sand on open ground covers a vertical tubular nest, which can be closed by a small secondary lid (see Appendix Fig.1; similar as that described for *Seothyra shreineri*; Purcell 1903). The silk-lined burrow is connected to the surface web which has extensions that radiate out to several entrances. A curtain of sticky silk threads covers the lip of each entrance, which opens into a little sickle-shaped depression in the sand. Under the web, the spider moves about upside-down with its feet in contact with the web. Several strong silk strands are strung loosely over the surface of the web and nest silk. Their position and orientation suggests that they could be signal threads that connect the web entrance with the tunnel base. The degree of wind exposure appears to affect web size and configuration. Winds exceeding 5m/s obliterate the entrance depressions and deposit sand onto the capture threads, thereby reducing spider foraging efficiency.

Crawling prey (small arthropod) is captured when it slips into one of the depressions and gets entangled in the capture threads. The spider then attacks and pulls it into the web entrance to entangle it further before biting. Immobilized prey is disentangled from the capture threads and is pulled under the web, usually head-first to prevent reentanglement. From there it is usually transported down to the base of the nest tunnel where the remains are stored.

In the Namib dunes, nests of *Seothyra* are locally abundant at dune bases and at moderate surface slopes between interdune vegetation hummocks. Wind exposure, surface slope and sand stability appear to affect web size and configuration and may be important limiting factors in determining the suitability of a particular location for constructing a functional capture web. The exploratory behaviour of released spiders on the sand surface suggests that the surface substratum of potential nest sites is tested before being selected.

2. Progress Report January 1988

Activity pattern in relation to temperature of buck-spoor spiders *Seothyra* sp. (Eresidae) in the Namib Desert

Introduction

During the first phase of collaborative work carried out in December 1987, we tested the hypothesis that:
H1: Nests of *Seothyra* meet their thermoregulatory requirements.

Spiders monitoring signal threads that join active entrances may need physical protection from diurnal surface temperatures of upto more than 70°C. The web of finely woven silk could serve as heat shield and/or the tubular burrow could be a heat refuge. Spiders may regulate body temperature by choosing different locations along a temperature gradient under the web mat and inside the burrow (Humphreys 1974). By utilizing this range of temperature provided by the complex web structure, spiders can remain active for longer periods of time.

From this hypothesis it can be predicted that: (a) spiders should be found in different parts of the web at different times of the day, (b) the range of temperatures actually experienced by a spider should be less than the range of temperature available at different locations in the web and burrow, and (c) spiders should continue to forage during periods when temperature conditions at web entrances are unfavourable.

Research Schedule and Personnel

Dr.Lubin visited the Desert Ecological Research Unit between 12 December 1987 and 8 January 1988. During this period, 23 days were spent conducting fieldwork with Dr.Henschel, who followed this up with a further 6 days of fieldwork. It is envisaged that this concludes fieldwork for the initial part of this project.

Dr.Seely coordinated research personnel and gave advice. Ms.A.Hornby assisted in the field. Extensive assistance with instrumentation and data logging was given by Messrs.F.Malan and S.Celliers.

Study Area

Most fieldwork was conducted on dune sand 1km SW of the Desert Ecological Research Unit (23°34'S/15°02'E) bordering the upper floodbanks of the Kuiseb River. This region had a known high density of spiders and was located within a 0,75 ha exclosure, fenced to exclude domestic livestock. Three relatively flat (<10°) stretches of sand (each 200m^2) were selected for intensive study. These areas had scattered small tufts (height <0,3m) of *Stipagrostis lutescens* and *Centrapodium glaucum* grass and diverse animal communities of riverine and dune origin. One area was exposed daily to strong afternoon winds which closed *Seothyra* web entrances. Two other areas were relatively sheltered from wind by adjacent clusters of *Acanthosicyos horrida*, *Acacia erioloba*, *Euclea pseudebenus*, *Tamarix usneoides* and *Salvadora persica*.

Research Outline

Nest Activity: Spider webs in the three selected areas were monitored daily for 24 days to determine the pattern of individual activity and nest tenure. For each web, the width of each open entrance bearing sticky capture threads was measured (±1mm) as an index to the degree of spider activity. Upon completion of the study, the size of each web (N=214) was measured. The diameter of the tube opening, or the width of silk connecting the web with the tube (±0.1mm), served as indices to spider size, using relationships determined by Henschel (unpubl.data).

Spider Attack Response: We monitored activity patterns of a sample of spiders from the three areas at 4h intervals over three separate periods of 24h each at weekly intervals. Webs were recorded as being open or closed. We assessed the spiders' readiness to respond to a prey stimulus by lightly stroking the capture threads with a fine bristle and measuring the time (≤15s) required to elicit an attack. Degree of activity of spiders was compared to differences in wind regimes of the three areas determined with wind totalizers (Wilhelm Lambrecht GmbH, Göttingen) and thermal depth profiles of nests (see below).

Nest Temperatures and Thermal Profiles: We tested the hypothesis that the capture web insulates the spider thermally and that the temperature inside the burrow is cooler by day than that of the surrounding sand. We recorded temperatures using copper-constantan type-T thermocouples, which were placed directly on top of and below the centre of a spider web and beneath 1mm of open sand next to the web. Temperatures were measured at intervals throughout four days using a Bailey Bat instrument (Sensortek Series 4, Model BAT-12).

In a second series of measurements, we used a field portable computer (Radio Shack TRS-80, Model 100) with reference junction and amplifier coupled to a A/D converter (Model ADC-1) to record temperatures from upto 16 thermocouples simultaneously at 15 min intervals over 24h-periods. We inserted a probe with thermocouple sensors at 1, 5 and 9 cm depth into a *Seothyra* burrow from which the spider had been removed. Another series of vertical thermocouples measured sand temperatures at the same depths adjacent to the nest. This was duplicated with thermocouples that were laid horizontal for 10cm from the terminal sensor to reduce possible effects of thermal conductance through the thermocouple. These readings were compared with two probes inside rigid plastic tubes (3mm diameter) with sensors also at 1, 5 and 9cm depths placed vertically into sand to simulate a burrow. One tube was covered on top with a *Seothyra* surface web and the other remained exposed. This experiment was repeated at two different locations over 24h periods.

An initial examination of results revealed that the probes inside plastic tubes covered or not covered with a web compared well with the nest probe. The latter was used for further measurements of temperature profiles at 0.1, 1, 3, 5, 7, 9, 11, 13 and 15 cm depths during four 24h records. Two additional thermocouples were placed on top of and below the centre of a surface web. In one experiment, temperatures recorded with this depth probe were compared with a probe inside a *Seothyra* nest. In another experiment the possible influence of thermal conductance along thermocouples to surface web temperature records was tested. Three thermocouples were placed under the same web with 13cm terminal lengths of each covered by 1mm of sand, *Seothyra* surface web, or a folded cardboard strip respectively.

<u>Upper Thermal Tolerance Limit</u>: We determined the temperature at which spiders began showing signs of heat stress. Newly captured spiders (N=17) were measured and placed into shallow (25mm deep) plastic cups (52mm diameter) containing 0.5cm of dune sand in the laboratory. The spiders constructed capture webs, but were unable to dig vertical burrows which could have acted as thermal havens. The following day, we placed these cups into direct sun at noon and monitored the temperature of the capture web. We recorded the temperatures at which vigorous movements by the spiders under the webs were evident and terminated the tests when spiders emerged onto the surface.

In another experiment, eight spiders were removed from their nests and released on open sand (>1m from closest grass) at different temperatures from early morning to noon. Temperature was monitored 0.1mm below the surface sand and 3cm off the ground in the shade of a grass clump. We recorded spider activity and distance moved until a nest was constucted or the spider took refuge in shade off the ground.

<u>Prey Handling Time</u>: The duration taken to remove captured prey from the surface may depend on prey size and type, the time taken by the prey to become immobilized from toxin and/or thermal stress and the spider's ability to disentangle the prey and manipulate it in such a way as to prevent reentanglement when it is pulled under the web. Temperature could influence the spider by affecting its degree of agility and by restricting the duration of its surface activity bouts (unbroken period of time spent at the web entrance). In order to observe prey handling behaviour in relation to surface temperature, we placed live prey onto capture threads parallel to web entances. Spider and prey activities were classified as shown in Table 1. The spider's actity and exact location inside the nest was unknown except when it moved about vigorously under the web or was active at the entrance. Adult mealworms *Tenebrio molitor* and natural prey, *Camponotus detritus* ants, were used as bait in 34 and 19 separate trials respectively. The ability of prey to escape following the spider's initial attack, after which the spider was prevented from manipulating the prey, was tested over periods of 2 min with 8 prey animals at dusk (moderate surface temperature).

Table 1: Classification of behaviour of spider and captured prey.

Spider
N = no response in 1 min
A = attacks
P = manipulates and pulls prey
H = holds prey down
M = moves under web
V = visible away from prey
U = location unknown

Prey
E = escapes
S = struggles strongly
W = struggles weakly
I = immobile
D = begins disappearing
G = gone under web
F = observations stop

Spider Thermoregulation: We considered a variety of possible techniques of estimating spider temperature in the nest and observing behavioural thermoregulation.

a) Direct temperature measurements of a spider in the field were unsuccessful. One of the biggest spiders found was glued to thin-guage thermocouple wires (Type TW40) and released into a nest, but could not move about freely with the added load.

b) Three methods of observing spiders in their nests were tested in a laboratory set-up. A spider was allowed to build a nest in a terrarium between two glass sheets or inside transparent plastic and glass tunnels, which were offered to the spider as artificial burrows. These were either not accepted by the spider or we could not ascertain the location of the spider inside the nest with certainty. Further attempts are being made.

c) Currently we are considering a variety of techniques to detect the location of the spider using radio-active, metal and magnetic sensors, but, to date, none are sensitive enough to detect the minute load that a spider is capable of carrying.

d) Temperature simulations of observed prey handling times were carried out with model spiders (freshly killed spiders coated with plastic spray) fitted with thermocouples. The experiment was designed under the assumption that an observed spider quickly went to the coolest place (35°) at the base of its nest when not observed in the hot web (65°) during prey capture. The model spiders were thus alternately placed between hot and cool locations using time schedules actually observed in the field. Mean, maximum and minimum temperatures were recorded. At the end of each trial, the lag time for the model to reach ambient temperature (hot and cool) of each location was determined.

Table 2: Data collected on *Seothyra* during Dec 1987 and Jan 1988.

Type	days	nests	data sets
Nest Activity Check	24	217	3727
Spider Attack Stimulus	3	200	2988
Temperature: Surface & Web	4	4	44
Temperature: Nest Profiles	6	4	7973
Heat Stress: Exposures	2	–	17
Releases	1	–	8
Prey Handling Times	3	53	53
Prey Escape after Attack	1	8	8

Initial Results

A total of 204 nests were monitored. In our three study areas, *Seothyra* population densities were 0.35, 0.265 and $0.425/m^2$ in areas A and C (wind-sheltered) and B (wind-exposed) respectively. Most individuals were active daily, others reopened their capture webs after 1-3 days of inactivity. During the study period 13.2% (27) of the websites became unoccupied of unknown causes. Incidental observations indicate that interference from birds, nocturnal gerbils and heteropodid spiders (*Leucorchestris arenicola*) may influence the location and tenure of web sites in this population of *Seothyra*.

Spiders were most active and showed greatest readiness to strike at a prey stimulus during the warmer hours of the day before the onset of wind, which closed the web entrances. At night and in the early morning, response time to a prey stimulus usually appeared to be longer than during the day.

Handling times of prey were shortest during the hot period of the day. At sand surface temperatures of >55°C, spiders attacked beetles within 2-3s, and had surface activity bouts of $\leq$10s. If the prey became entangled in the silk and could not be pulled into the web directly after the attack, the spider made repeated attempts to retrieve it, each attempt lasting only a few seconds. We infer from this behaviour that the spider thermoregulates during prey capture by shuttling between the hot capture web and the cool tunnel base.

Temperatures directly on top of and below the centre of a web and on the sand surface next to it were similar. We conclude that the capture web does not insulate the spider thermally. It does, however, protect the spider from direct radiation. Release experiments showed that spiders can survive on the surface in shade at sand temperatures that exceed 50° but cannot do so in direct sunlight.

While spiders may attack and subdue prey at surface temperatures that exceed 60°, they showed distinct thermal stress at 48-51°C when unable to burrow. Thus, the burrow apparently serves as a means of rapidly dissipating the heat load that the spider takes on while active beneath the capture web.

We were unable to determine the exact location of a spider inside its burrow. We attempted to measure spider body temperature directly in the field by attaching a fine thermocouple wire to it. This was unsuccessful because the wire disrupted the spider's activity. Indirect methods using spiders in the laboratory are planned.

3. PRESENTATIONS

A poster on the thermoregulation work was presented at the 2nd Colloquium of the Research Group for the Study of African Arachnids, held in Swakopmund during July 1988. An initial analysis of data was performed, which provided an opportunity to prepare a synopsis of the present study (Appendix).

It is envisaged that the first draft of this paper will be prepared before January 1989. This would enable joint discussion and redrafting during Y.D.Lubin's next planned visit to the Namib. This paper is intended for submission to the Journal of Arachnology or the Journal of Arid Environments.

4. CURRENT RELATED RESEARCH ON *SEOTHYRA*

Spider Activity: Ms.A.Hornby and Ms.C.Parkinson are assisting J.R.Henschel in monitoring *Seothyra* activity (by measuring length of trapping areas) from some 200 nests in the three sample areas at Visnara. Checks are carried out weekly from December 1987 at least until February 1989. Occasionally, nests for which occupation status is doubtful, are excavated. Bimonthly, web size, tunnel diameter and distance to nearest neighbours are measured. All data are loaded onto computer immediately upon return from the field.

Population Structure, Density, Reproduction and Diet: From February 1988 to February 1989, surveys of three distinct *Seothyra* populations are carried out bimonthly. One site is adjacent to the main study area at Visnara (for the above work), another is a dune site at !Khomabes, 8km from Gobabeb, while the third is on the sandy upper floodbanks of the Kuiseb River. At each site, 8 noncontiguous sample blocks of 10x10m are selected randomly each time. All *Seothyra* nests are excavated to measure nests, capture spiders and to collect prey remains. Spiders are examined, sexed, measured (with calipers or microscope) **and** weighed ($\pm$0.1mg) in the laboratory and released at the capture site at dusk. J.R.Henschel is assisted by A.Hornby and C.Parkinson in field, laboratory and computer tasks and by I.Henschel and M.van Greune in the field. I.Henschel assists in the identification of prey by comparison with voucher specimens.

Natural History: Data on habitat selection and distribution has been gathered. Descriptions of nest structure are qualified from careful dissections of nests. The various types of silk are identified crudely and related to their utilization. This will be presented together **with** all observations of the behavioural repertoire and life history trends recorded in other parts of the study.

Other Collaborative Studies

Three other projects on *Seothyra* were initiated by other researchers in collaboration with us upon commencement of the present investigation in the Namib. These are:

1) Dr.Ansie.S.Dippenaar of the Plant Protection Research Institute, Pretoria, South Africa, is revising the taxonomy of the genus *Seothyra*. Material from the Namib collected by us is being included in this revision. This should lead to the description and naming of the subject of the present study.

2) Prof.Dr.Hans Peters of the University of Tübingen, West Germany, is planning to examine the microstructure of the capture threads and other silk, as well as their production from various silk glands of *Seothyra*, by scanning electron microscopy in close collaboration with us. Nest material has already been sampled, carefully packed and posted. Under the guidance of H.Peters, spinnerets of *Seothyra* in the Namib will be fixed with wax during various phases of silk production for careful analysis in Tübingen.

3) Dr.Scott Turner of the University of Cape Town, South Africa, has drawn up a model to estimate **the** temperature of *Seothyra* handling prey in the hot web. Further progress on this model should be made during Drs.Lubin and Turner's next visit to the Namib (see section 5C on Page 13).

5. FUTURE COLLABORATIVE RESEARCH IN THE NAMIB

A: Web construction and foraging behaviour of *Seothyra* sp. in the Namib Desert

Introduction

The next phase of our collaborative investigation of *Seothyra* sp. will involve testing of the second hypothesis that:
H2: Web structure is primarily determined by foraging requirements.

This implies that nests are designed to meet the requirements for capture of sufficient types and numbers of prey, which may determine the number, length and relative spacing of active entrances, which are lined with sticky capture threads. Adjustments of trapping area to prey availability were observed in orb-weaving spiders (e.g. Witt et al, 1968). Prey capture success of *Seothyra* needs to be compared with the cost of maintaining these traps open against regular shifts of surface sand in variable wind conditions.

The cost of silk nest construction may be very high if continual repairs are required (Lubin, 1973; Prestwich, 1977). This cost consists of the metabolic cost of activity plus the cost of the silk itself. The cost of producing cribellate silk is assumed to be greater than that of producing non-cribellate silk (Lubin, 1986). However, there are no measurements of the cost of web construction in any cribellate spider. We will compare the two components of the cost of web-building (silk and activity) in two manipulated groups of food-deprived and well-fed spiders.

Research Plan

Wind appears to have a pronounced effect on the ability of *Seothyra* to forage and, presumably, on the cost of nest maintenance. This effect can be assessed by monitoring unprotected (no wind shield and clear of vegetation) webs and comparing them to equally-sized neighbouring spiders with wind-shielded webs (erect barrier on upwind side only). The wind-strength factor will be standardized for the main experiment.

We intend to manipulate prey availability to determine if this influences the number, length and distribution of trapping surfaces in the web. It is predicted that costs of web construction and maintenance are inversely related to prey availability because: (a) when prey availability is reduced, spiders should increase the trapping area by creating more entrances, longer trapping threads, or both; (b) when prey are abundant, spiders should utilize fewer trap entrances and reduce the amount of time spent in web repair.

The efficacy of using a low wall of synthetic material covered with a very light netting that constitutes a barrier to small crawling arthropod prey will be tested. It is necessary that this wall is effective in keeping all such arthropods in or out of the enclosure and to prevent spiders from escaping. The response time (if any) of the spiders will determine the minimum length of the experiment described below.

We will prevent insects from entering one group of webs by constructing barriers around the webs. Another group of webs within similar enclosures will be provided with extra prey. An unmanipulated group will have the barrier slightly raised above the ground to allow prey to enter unhindered, but should serve as a similar wind protection as the manipulated webs. The control group will have no barrier in the vicinity of the webs. At the onset of the experiment, all spiders will be removed from their original nests and released to construct new nests. For each nest we will monitor: (a) the number of prey caught, (b) numbers and total length of active traps, (c) the trapping area, and (d) web repair activity. All nests will be reopened at the termination of the experiment to confirm number of prey caught from nest contents, to obtain below-ground measurements of burrows and to sample nesting material for further analysis.

As a measure of the amount of silk contained in a nest, we will weigh oven-dried cleaned (all organic debris removed) burrows and surface webs separately, before incineration in a muffle furnace or bomb calorimeter and reweighing of the inorganic remains. This will enable us to separate the mass of silk from the sand bound to it and to estimate the energetic content of the silk (Lubin, 1973). The total cost of the silk can thus be estimated. Eresid spiders are not known to recycle old silk during web building so that any error due to underestimating the amount of silk produced by the spider can be discounted. The cost of activity during web construction can be estimated under laboratory conditions by measuring metabolic rates using standard respirometry techniques (e.g. Prestwich 1977). From our field observations of activity, we will estimate the amount of time spent daily in web maintenance. From these data, the average daily energy cost of web-building can be calculated.

<u>References</u>

Lubin, Y.D., 1973. Web structure and function: the non-adhesive orb-web of <u>Cyrtophora moculuccensis</u> (Doleschall) (Araneae: Araneidae). <u>Forma et Functio</u> 6: 337-358.

Lubin, Y.D., 1986. Web building and prey capture in the Uloboridae. In: W.A.Shear (ed.) <u>Spiders: Webs, Behaviour and Evolution</u> pp 132-171, Stanford University Press.

Prestwich, K.N., 1977. The energetics of web-building in spiders. <u>Comp.Biochem.Physiol.</u> 57A: 321-326.

B: Anti-predatory behaviour by *Seothyra* in the Namib Desert

Introduction

The third hypothesis that we will test is that:
H3: The web-building behaviour, nest structure and appearance on the surface of *Seothyra* relates to its anti-predatory function.

Seothyra that wait for prey among an array of capture threads require concealment and physical protection against spider predators. These could be birds, lizards, geckos, gerbils, pompilid wasps, heteropodid spiders, solifugids or scorpions, all of which are known to occur in the same habitat as *Seothyra* in the dunes. Extensions of the *Seothyra* web, which is concealed below a thin layer of sand, could serve to keep the spider at some distance from active entrances, which could serve as visual cues to spider predators. The ability to take refuge in a burrow which can be closed by a secondary lid and by some degree of constriction may provide extra protection.

Although *Seothyra* could have potent venom (Lawrence, pers.comm.), which can subdue insects and conspecifics in less than 30s after a deep bite (pers.obs.), its effect on potential predators has not been observed. One large pompilid wasp has been collected as prey from an excavated nest, indicating the possible invulnerability of this haven to such a potential predator. Several nests in the study area have been destroyed by gerbils and birds, indicating that *Seothyra* in nests are occasionally selected as prey.

The only *Seothyra* that we have seen moving about freely in broad daylight have been adult males. The close resemblance of these males to sympatric *Camponotus* spp. ants, which are aggressive and apparently not preferred as prey by some potential predators (such as dune lizards (R.D.Pietruszka, pers.comm.) or dune larks (H.Boyer, pers.comm.)), could be a case of protective or Batesian mimicry.

Research Plans

Since predation is rarely observed (possibly due to the protection by nests and also due to disturbance of predators by observers), an artificial measure of potential pressure exerted by predators must be obtained. Some demographic changes recorded in the annual population study at Visnara and the bi-monthly censuses could serve as indicators to mortality rates.

In the present investigation, we propose to 'stake out' dead or restrained spiders for short durations or use similar-sized insects or synthetic painted models of spiders that can be securely pinned down. These will be placed (a) on or near webs of *Seothyra* or (b) concealed under webs with no sand cover to facilitate detection and (c) concealed under normal webs that are covered by sand except at open entrances. The proportion of spiders found and taken by predators will provide an estimate of maximum predator pressure on exposed and concealed spiders. By observing these prey from a hide, or examining tracks left in the sand, information on the identity of predators can be obtained.

The behaviour of live spiders released on the sand surface during periods of moderate climate (no wind, temperature around 25°C, no direct sunlight; such as at dusk) will be monitored closely. We will determine the time after release and distance moved from the release site until concealment under a sheet of silk and sand. This would indicate the degree to which exposure to predators is avoided at a time when climatic effects should not restrict surface activity of spiders.

The suggestion of adult males displaying Batesian mimicry is best investigated by direct observations. As adult male *Seothyra* appear to occur only in early winter (May-July), we plan to extend this part of the investigation into the following winter. Nests of subadult or adult males (similar in appearance to those of adult females) will be identified prior to their departure. A confining barrier will be placed around such nests to prevent males from wandering off during an observer's absence. Nests will be checked daily and food provided weekly. Emerging males will be freed and observed from a hide for the duration of their wanderings in search of mates. It is hoped that this should reveal their possible relationships with other species, particularly the mimicked ant species and potential predators.

C: Body Temperature in a Shuttling Spider

Introduction

Can *Seothyra* gain extra time to subdue prey by engaging in shuttling between the hot trap (web) and the cool burrow? In consultation with us, Dr.Scott Turner of the University of Cape Town, South Africa, has drawn up an outline to model the temperature of spiders handling prey in a hot web, a factor that could not be determined by us in our study of *Seothyra* thermoregulation. Initial computer modeling simulating has been run. J.S.Turner and we plan to carry out fieldwork, discussions and to draw up plans for constructing a practical model simultaneous to our other investigations in the Namib.

Research Plans

We will measure cooling rate and heating rate of different sizes of spiders. Fine thermocouple wires are glued to the carapace and spiders moved into regions of known hot or cold temperatures. Video monitors of a stop-watch next to a Bailey Bat will enable us to measure rates accurately. This will enable us to calculate a heating curve for the spiders observed during prey subjugation in hot traps.

Prey handling experiments similar to those carried out already will again be conducted with emphasis on hotter periods of day. As the accuracy of timing activity schedules of actual activities with stop-watches is limited, the process of prey handling should be filmed on video. These will be closely analyzed to obtain accurate prey handling schedules. Subsequent measurements of spiders and their nests will enable calculations of their heating rate constants and to estimate the distance traveled up and down during the process of prey subjugation. This should enable to estimate the costs and benefits of shuttling behaviour in *Seothyra*.

6. FUTURE COLLABORATIVE RESEARCH IN THE NEGEV

Web construction and thermoregulation of Stegodyphus sp. in the Negev Desert

Introduction

The eresid genus Stegodyphus contains numerous species adapted to desert environments. Many of these are subsocial to highly social, and it is this aspect of their biology that has been the focus of most studies (e.g., Ward 1986, Wickler and Seibt 1986). Stegodyphus species build exposed webs, often placed high in shrubs or trees. The web consists of two elements: a sticky trap for flying insects and a nest or retreat 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 web constitutes the major adaptation of Stegodyphus to arid environments. Therefore, to understand how Stegodyphus species have radiated in this environment, it is necessary to understand the structure and function of its web.

In the Negev desert, Stegodyphus sp. spiders build conical or tubular nests near the top of shrubs (Levy 1985). The capture web radiates from the mouth of the nest in a two-dimensional array of non-sticky, radial elements and sticky (cribellar) connecting silk threads. The web has the appearance of an untidy orbweb and is designed to trap flying insects. The nest itself is made of very dense and woolly silk, with remains of prey (insect exoskeletons) and other debris embedded in its walls. The web of Stegodyphus is a complex and energetically expensive structure; it is unlikely that spiders relocate their webs frequently. Given that the spiders may live two years (Levy 1985), we expect that (1) they will select websites with regard to those factors which are most critical in the long-term, and (2) they should be able to make adjustments of their webs and behavior to accommodate short-term environmental changes.

Stegodyphus nests superficially resemble those of the desert widow spiders, Latrodectus revivensis and L. pallidus (Theridiidae), which occur commonly in the Negev. These, too, are conical, debris-covered structures, suspended near the tops of shrubs (Shulov 1948, Lubin et al. in prep.). This prompts the question whether this is a case of convergent evolution of nest structure (theridiids and eresids are widely separated phylogenetically), designed to meet certain physical and biotic requirements of desert environments.

In parallel with our investigation of Seothyra nests, we propose that Stegodyphus web structure may be determined primarily by microclimate requirements (hypothesis 1), foraging requirements (hypothesis 2), or protection against predators and parasites (hypothesis 3). We will test these hypotheses by examining predictions deriving from them.

The first hypothesis predicts that the nest provides physical protection from radiation in summer, and a range of temperatures that allow the spider to reduce its heat load through behavioural thermoregulation. Based on hypothesis 2, we predict that the location of nests in shrubs and the design features of the capture web maximize the spider's ability to intercept and trap flying insects. Hypothesis 3 suggests that the nest protects the spider from potential predators, either through mechanical protection of the silk and debris, or by camouflage.

Research Plan

The study is planned to take place during the months April-May. The study site is 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. The area is arid, with winter rainfall that averages 92 mm annually and is highly variable from year to year, both in quantity and in temporal distribution (Evenari et al. 1982). The vegetation on the rocky slopes consists of scattered, perennial shrubs of less than 1.5 m height (*Artemesia* spp., *Zygophyllum dumosum*, *Noaea mucronata*, *Hammada salicornica*, and others), and numerous annuals and geophytes which occur seasonally. Adults and larger instars of *Stegodyphus* are found on shrubs on these hillsides in spring and early summer. Throughout the summer, mostly juveniles are present.

Because of time constraints, we will not be able to test all three hypotheses mentioned above. Instead, we propose to examine in detail one of these (hypothesis 1). By doing so, we will obtain results that will be comparable to those obtained from studies of *Seothyra* sp. in the Namib desert, as well as to results of a similar study of the desert widow spider, *L. revivensis*, in the same habitat as *Stegodyphus* (Lubin et al. in prep., Zilberberg 1988).

We will test the following predictions of hypothesis 1:

1) Webs of *Stegodyphus* are built on shrubs in such a way as to reduce the heat load on the spider during the hot months.
2) The nest provides a range of temperatures. Spiders thermoregulate by moving along a temperature gradient in the nest.
3) The onset and duration of predatory activities depend on ambient and nest temperatures.
4) Spiders in thermally unfavourable websites will be less active in prey capture, and will obtain less food, than spiders in thermally more favourable sites.

Web position. -- Spiders should construct their nests high in shrubs during the hot season to reduce heating due to re-radiation from the substrate and to take advantage of cooling air currents. In addition, nests should be positioned in such a way as to be shaded by the shrub during periods of maximum insolation. We will measure the height, aspect, and orientation of nests in shrubs in a sample of webs of *Stegodyphus*. We will obtain temperature profiles at different heights above the ground, and in different locations within shrubs (see below).

Nest temperatures. -- We will use fine copper-constantan thermocouples inserted into spider-sized models of solid aluminum (a good conductor of heat) to measure temperatures at different locations inside nests of *Stegodyphus*. Temperature measurements will be recorded on a datalogger in the field and transferred to a computer in the laboratory. We will compare the rates of heating and cooling, and maximum temperatures attained at different locations within the nest against standard air temperature.

Spider thermoregulation. -- The problem of determining where *Stegodyphus* sits inside its nest is similar to that of determining the location of *Seothyra* inside its burrow. The walls of the nest are opaque, and the whereabouts of the spider cannot be determined from the outside. Two possible techniques are: (i) providing artificial nests made of parachute nylon, through which the spider will be visible, and (ii) attaching small pressure transducers at different positions on the nest wall to determine movement of the spider in the tube. If we are successful, we will match spider locations with temperature profiles at different points in the nest. Other thermoregulatory behaviour of the spiders will be noted by direct observation.

Spider activity. -- We will assess prey capture activity in a sample of spiders by observing their response to an artificial prey stimulus (vibration of the capture web). As with *Seothyra* sp. in the Namib, we will measure the time it takes spiders to respond to the stimulus and we will record other conditions prevailing at the time (ambient temperature, wind velocity). We will compare activity levels of spiders at different times of day and at different websites to test for direct effects of microclimate on activity. In addition, spiders will be tested with live insects of common prey species at various times of day in order to measure the handling time of the spiders with different prey under different conditions.

Available Equipment.

Equipment and services available at the Institute for Desert Research at Sede Boqer include: a Campbell datalogger with sensors, a minicomputer for data reduction and analysis, microscopes, stereoscopes and balances, and a vehicle for field use.

References Cited

Levy, G., 1985. Plants and Animals of the Land of Israel: *An Illustrated Encyclopedia, Vol. 2, Terrestrial Invertebrates.* (In Hebrew).

Lubin, Y., Ellner, S. and Kotzman, M., In prep. Web structure in relation to possible website selection in a desert widow spider.

Shulov, A., 1948. *Latrodectus revivensis* sp. nov. from Palestine. *Ecology* 29:209-215.

Ward, P.J., 1986. Prey availability increases less quickly than nest size in the social spider *Stegodyphus mimosarum*. *Behaviour* 97:213-225.

Wickler, W. and Seibt U., 1986. Aerial dispersal by ballooning in adult *Stegodyphus mimosarum*. *Naturwissenschaften* 73:628.

Zilberberg, G., 1988. Behavioral Ecology of the desert widow spider, *Latrodectus revivensis* (Araneae, Theridiidae) Shappirit. *Journal of the Israel Entomological Center* 6:52-76 (In Hebrew).

7. APPENDIX

Synopsis of Poster presented at the 2nd Colloquium of the Research Group for the Study of African Arachnids, Swakopmund, July 1988

SEOTHYRA ACTIVITY IN RELATION TO TEMPERATURE

Abstract

In the Namib dunes, the nest of Seothyra sp. comprises a horizontal capture web on the sand surface that covers a vertical tubular burrow. Crawling arthropods become entangled in the sticky cribellar silk at the edges of the capture web and are attacked, subdued and pulled into the burrow by the spider. We studied the influence of nest temperature on the spiders' foraging behaviour. The spiders' response to prey stimuli and thermal profiles of nests were determined. Although often active at all hours, responses were quicker during the heat. The thermal stress threshold was about 49°C. When handling prey, spiders were slow at web temperatures below 40°C and quick above 55°C, despite the need to thermoregulate. Our study supports the hypothesis that nest design and behaviour enable Seothyra to hunt even under extreme thermal conditions.

Study Area

During December 1987–January 1988, we used three $200m^2$ plots of flat dune sand 1km SW of Gobabeb, where Seothyra burrows occurred at a density of $0.3/m^2$.

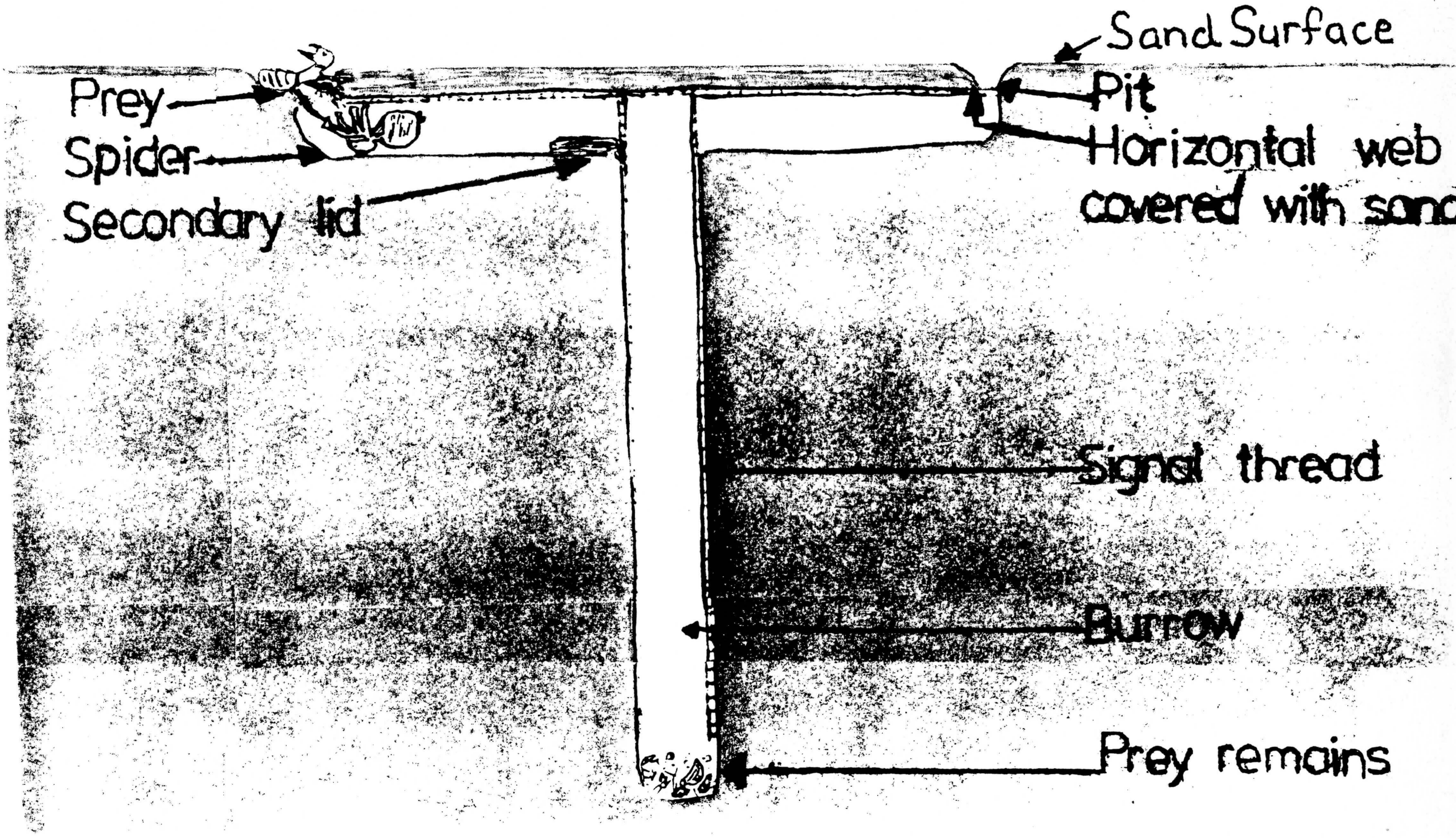


Figure 1: Schematic Representation of a *Seothyra* Nest Cross-Section

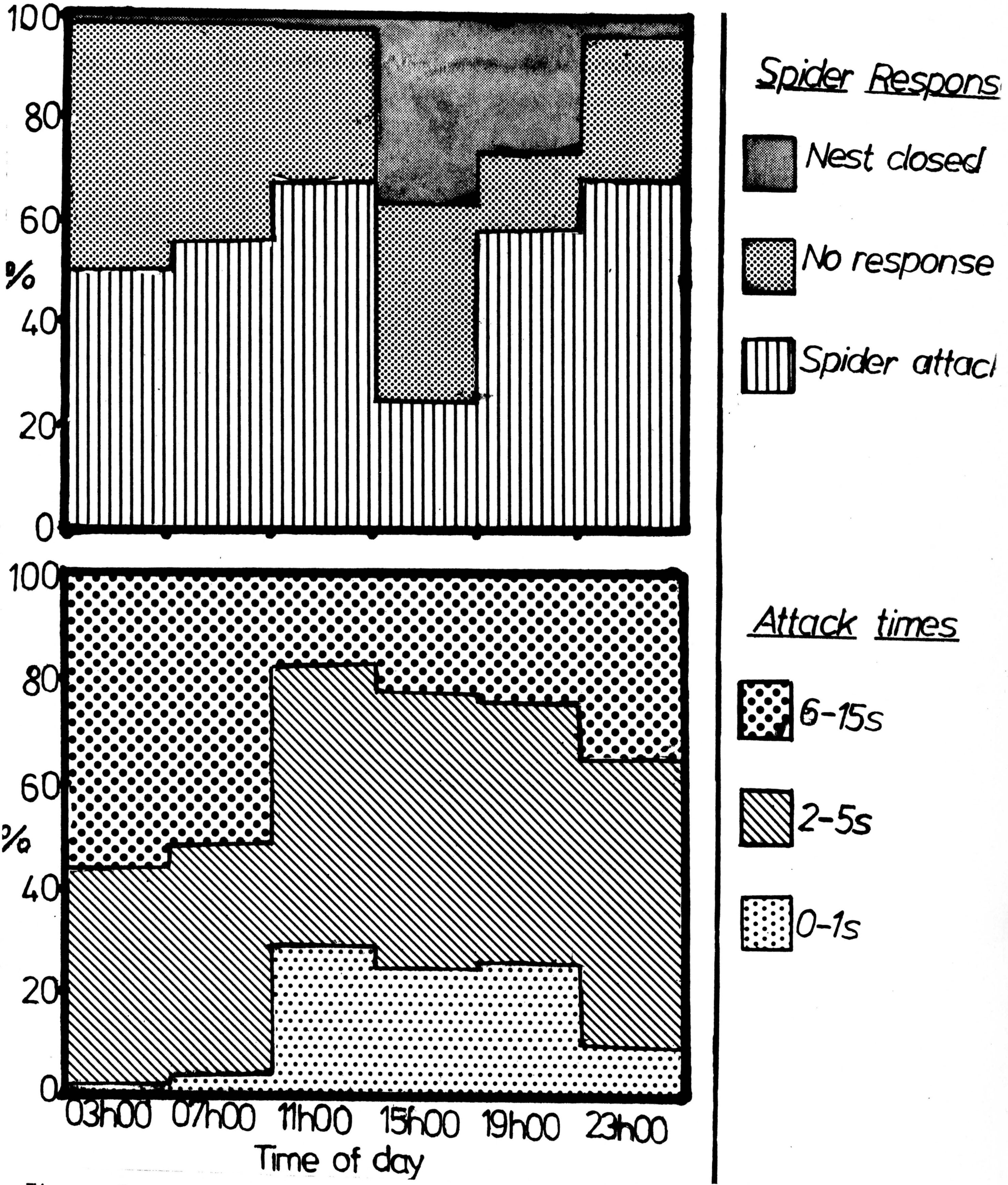
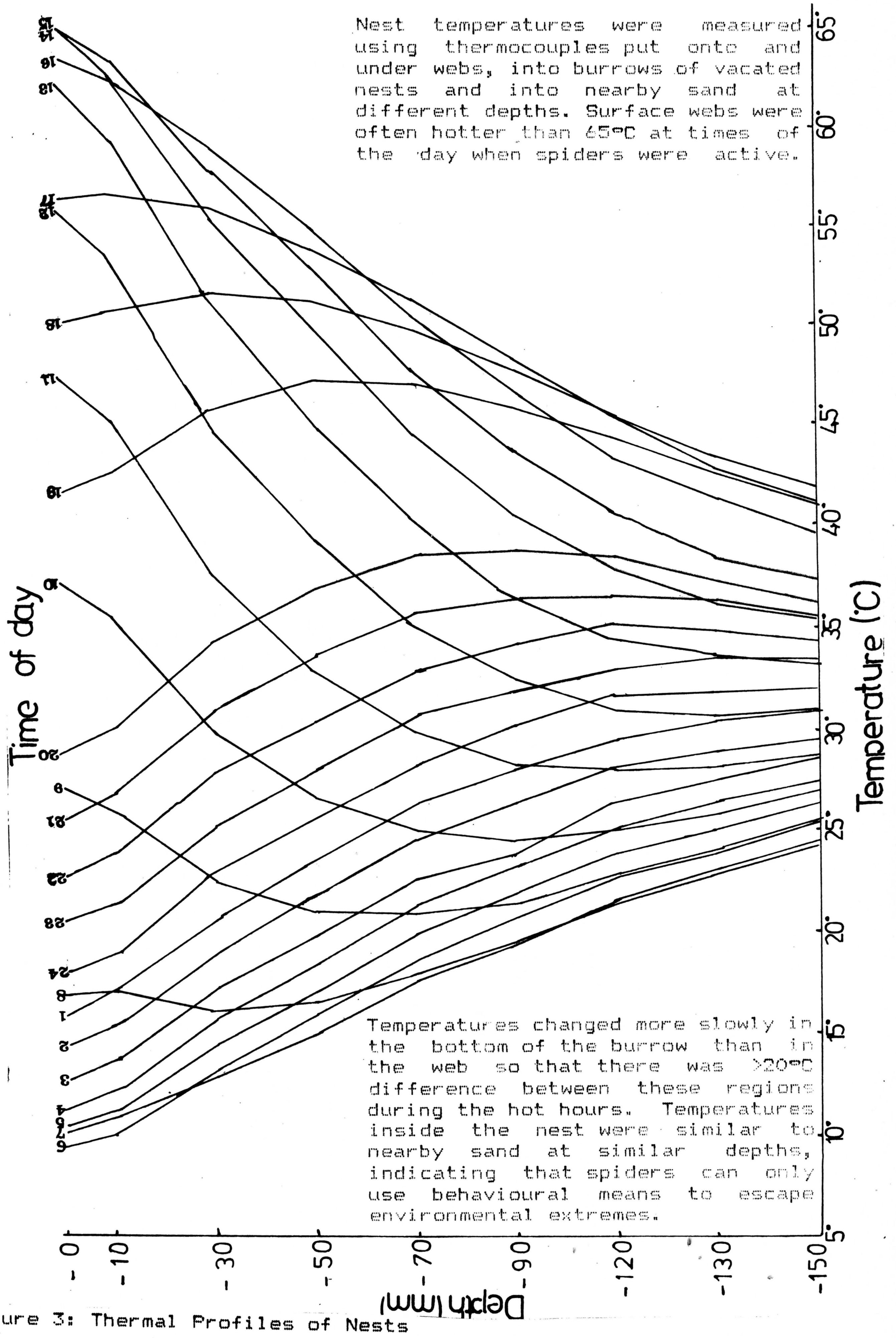


Figure 2: Attack Response
We simulated a prey stimulus by stroking the capture web with a fine bristle and measured the latency to attack at different times of the day in a sample of 200 spiders over a period of three days. Spiders responded at all times of the day. Fewer responded at 15h00, when strong winds covered the webs with a layer of sand. The latency to respond was shorter during the warm hours. From 11h00 to 19h00 more than 70% of spiders that responded did so in less than 5 sec.



Nest temperatures were measured using thermocouples put onto and under webs, into burrows of vacated nests and into nearby sand at different depths. Surface webs were often hotter than 65°C at times of the day when spiders were active.

Temperatures changed more slowly in the bottom of the burrow than in the web so that there was >20°C difference between these regions during the hot hours. Temperatures inside the nest were similar to nearby sand at similar depths, indicating that spiders can only use behavioural means to escape environmental extremes.

Figure 3: Thermal Profiles of Nests

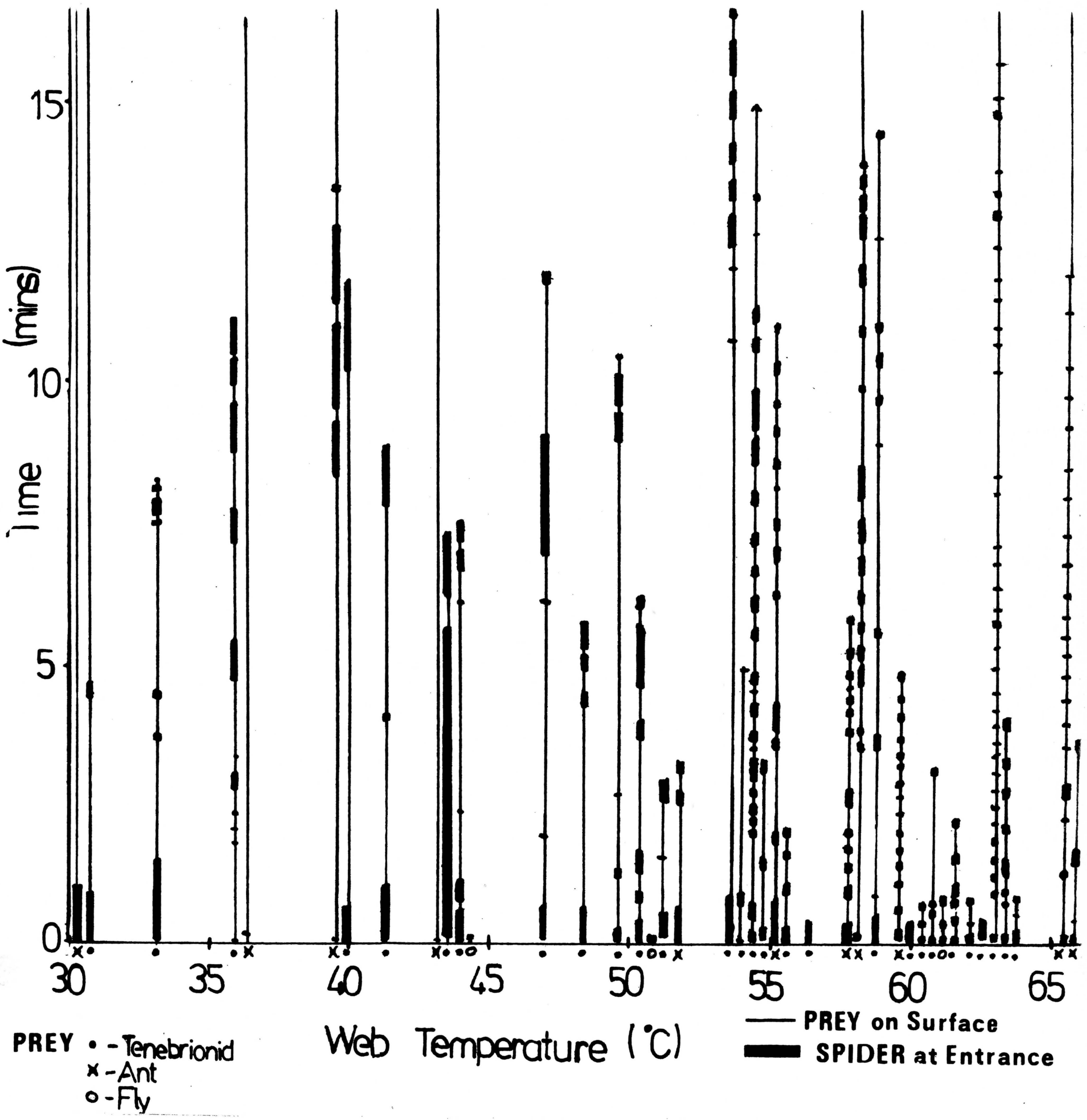


Figure 4: Prey Handling Time
We offered spiders different prey types (ants, beetles, flies) at different times of day and recorded the spiders' behaviour. We measured the duration of activity bouts at the web and the total time to subdue and remove prey from surface. We found that web temperature and prey type determined prey handling schedules, which were shorter during the heat. Above 55°C, spiders attacked prey within 2-3 sec, and had activity bouts at the surface of <10 sec. If prey was very entangled, spiders had to make repeated attempts to remove it. These attempts grew progressively shorter with time. Between activity bouts spiders probably cooled off deep in their burrows.

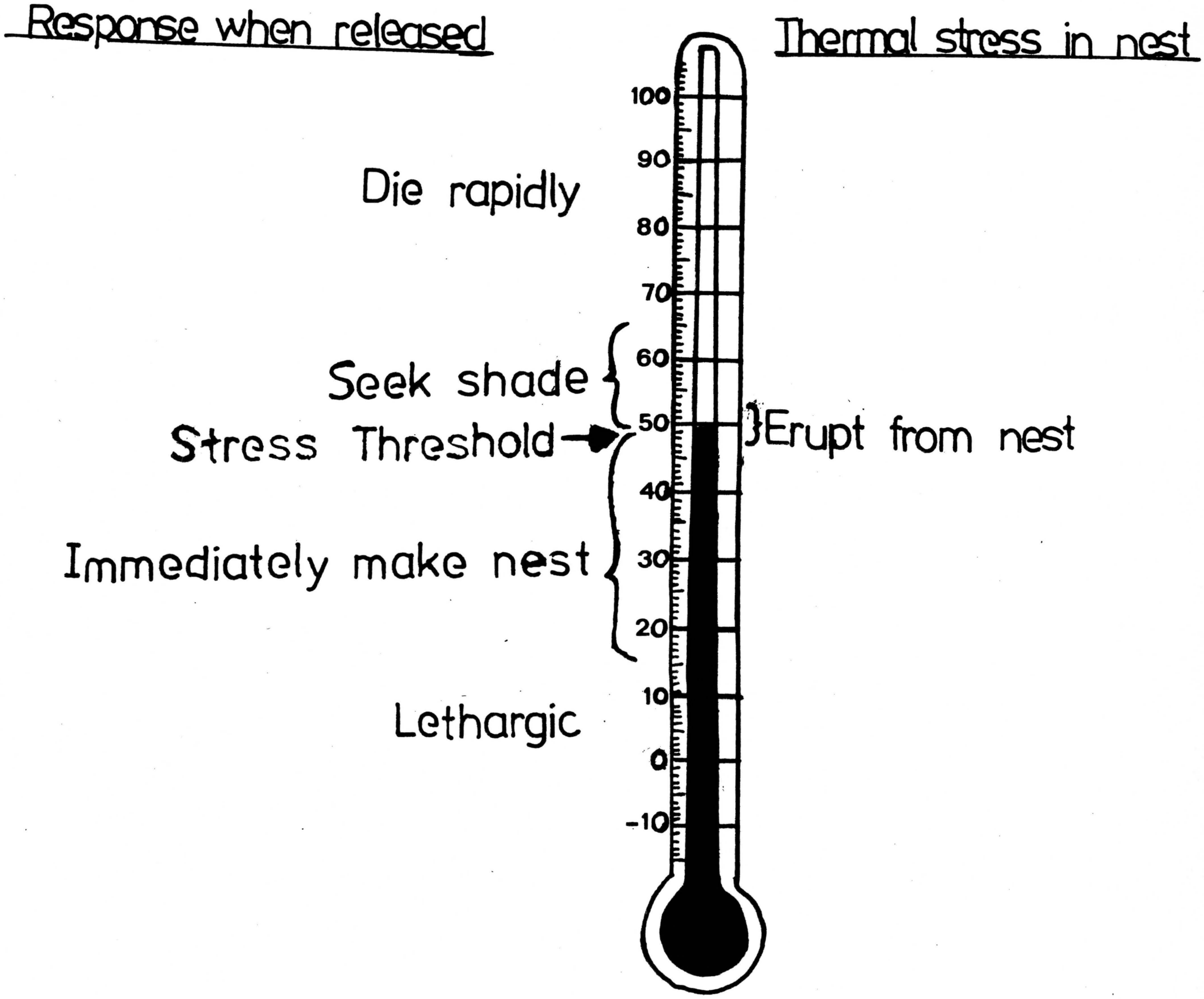


Figure 5: Upper Thermal Tolerance
Laboratory spiders were allowed to build 1cm deep nests in shallow containers. Temperature was monitored while nests were steadily warmed up until the spiders showed vigorous agitation and abandoned their nests. In another experiment, we released spiders on the sand at different temperatures and recorded the activity until spiders constructed a nest or took refuge in shadow. Spiders showed signs of thermal stress at 48-50°C. When released on the surface of the sand, they survived in the shade at sand temperatures that exceeded 50°C, but could not do so in direct sunlight.

Conclusion

Seothyra is a remarkably heat-tolerant spider. Although active at any time of day or night, response to prey stimuli and prey handling times were shortest during the hot periods of day. Despite an upper thermal tolerance limit of 48-50°C, spiders were capable of handling captured prey at web temperatures exceeding 65°C. It is suggested that spiders achieve this by shuttling between the hot web and the bottom of the burrow, where it is >20°C cooler. This enables *Seothyra* to forage at any hours when its prey is active.