

## Foraging at the thermal limit: burrowing spiders (*Seothyra*, Eresidae) in the Namib desert dunes

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**Summary.** In the Namib Desert dunes, the web of *Seothyra* sp. (Eresidae) comprises sticky silk lining the edges of a horizontal mat on the sand surface. The spider sits in a silk-lined burrow attached to the mat. Arthropods become entangled in the sticky silk of the mat and are attacked and pulled into the burrow by the spider. We investigated the influence of sand surface temperature on the activity of spiders during the summer. We determined the range of thermal conditions encountered by spiders, their temperature tolerance and the influence of temperature on foraging activity and prey handling behavior. The environmental temperatures available to *Seothyra* vary from 17–33° C at the coolest time of day to 33–73° C at the hottest. When prevented from retreating into burrows, spiders showed signs of thermal stress at about 49° C, whereas unrestrained spiders continued to forage at web temperatures above 65° C by moving between the hot surface mat and the cooler burrow. Spiders responded quicker to prey stimuli during the hot hours of the day and completed prey capture sequences in significantly less time at surface temperatures above 49° C than below. Furthermore, captured arthropods succumbed more quickly at high surface temperatures. Our study supports the hypothesis that web design and thermoregulatory behaviors enable *Seothyra* to hunt under extreme thermal conditions.

**Key words:** Web design – Behavioral thermoregulation – Foraging activity – Burrowing spiders – Eresidae

Arthropod activity is strongly limited by climatic conditions, especially temperature and humidity (Casey 1981; Crawford 1981; Willmer 1982). In spiders, high daytime ambient temperatures may restrict the time available for foraging on the surface, thereby influencing growth and reproductive output (Riechert and Tracy 1975). Many desert arachnids avoid extremes of temperature and the

risk of dehydration by sheltering during the day in burrows and being active at night when conditions are more favorable (Cloudsley-Thompson 1982; Humphreys 1987). Sit-and-wait predators adopt a different strategy by remaining in a retreat or burrow and foraging for prey that approach within striking distance. For sit-and-wait predators with permanent burrows, the risks of exposure to climatic extremes and to predation are reduced (Shachak and Brand 1983) and consequently, they may be able to continue foraging when climatic conditions on the surface are unfavorable.

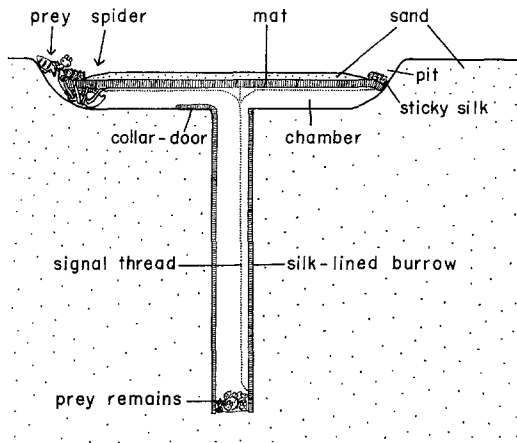
The dune-burrowing spider, *Seothyra* sp. (Eresidae), is a sit-and-wait predator that uses sticky silk on the surface of the sand to trap terrestrial arthropods. While foraging during the day, the spider remains concealed and shielded from direct radiation beneath a surface mat or within the burrow. In this study, we test the hypothesis that web design and thermoregulatory behaviors enable *Seothyra* to forage under extreme thermal conditions. We predict that: (a) the spider's physiological tolerance limits are adapted to its thermal environment, (b) the complex structure of the surface mat and burrow provides a suitable thermal environment, and (c) the spider may regulate its body temperature to allow foraging even when temperatures on the surface are unfavorable.

In order to test this hypothesis, we determined the thermal environment of the web of *Seothyra*, the spider's upper thermal tolerance limits and its prey-handling behavior in relation to temperature. Finally, we examined the foraging patterns of a population of spiders in relation to temperature and other factors.

### Materials and methods

#### *Natural history and study sites*

In the central Namib Desert, *Seothyra* sp. occurs commonly on open stretches of sand at dune bases and at moderate surface slopes (<20°). The web of this species is similar to that described for



**Fig. 1.** Schematic cross-section of the web of *Seothyra*, showing horizontal mat, chamber, sticky silk and vertical burrow

*Seothyra schreineri* (Purcell 1903). It comprises a dense silk mat overlying a horizontal chamber below the sand surface and a silk-lined, vertical burrow (Fig. 1). Lobes of the surface mat are lined with sticky silk and open onto semi-circular depressions in the sand. Arthropods become entangled in the sticky silk edges and their struggling alerts the spider via signal strands which extend from the mat into the burrow. *Seothyra* responds to a snared arthropod by running out under the surface mat, seizing the prey by its legs, then biting and pulling it down to further entangle it in the sticky silk. The immobilized prey is then pulled beneath the mat and into the burrow. Spiders used in this study were juveniles with total body length of 5–9 mm (body mass of 47 spiders =  $59.1 \pm 25.6$  mg). Adult *Seothyra* sp. attain body lengths of  $\geq 10$  mm (60–300 mg).

The study was conducted during December 1987–January 1988 and January–February 1989 at two study sites in the vicinity of the Desert Ecological Research Unit at Gobabeb ( $23^{\circ}34'S$ ,  $15^{\circ}02'E$ ). The main site (Visnara) was a stretch of dune sand at the edge of the Kuiseb river, 1 km SW of Gobabeb. Three areas of 200 m<sup>2</sup> each, within 20 m of each other, were selected for intensive study. These areas had scattered, small tufts of grass and a diverse arthropod community of riverine and dune origins (Crawford and Seely 1987), but differed in their exposure to wind. One area experienced strong afternoon winds, another was relatively sheltered by nearby trees, while a third area was intermediately sheltered. Another study site (Khommbabes) was on a sheltered, vegetated, transverse dune 5 km NW of Gobebe. Both study sites had high densities of *Seothyra* (1–10 per m<sup>2</sup>).

Statistical tests follow Sokal and Rohlf (1981). Means and one standard deviation are reported throughout.

### Thermal environment of the web

We monitored daily variation in temperature at different locations in the burrow of *Seothyra* and in simulated burrows in the sand and compared temperature depth profiles of burrows with those of the sand at the same depths.

Temperatures were measured with fine copper-constantan type-T (plastic-coated) thermocouples attached to a Baily Bat instrument (Sensortek Series 4, Model Bat-12), or later, to a portable computer (Radio Shack TRS-80, Model 100) with reference junction and amplifier coupled to an A/D converter (Model ADC-1). Using the latter equipment, we recorded temperatures at 6 s intervals and averaged these over 8 min. These measurements were repeated every 30 min at each burrow for approximately 24 h.

We performed the following comparisons:

(1) Temperatures on the surface of the mat, beneath the mat and 1 mm beneath the surface of the sand near the mat. Temperatures were recorded during the day over a 4-day period.

(2) Temperature profiles at different depths in burrows and in simulated burrows. Both were measured with thermocouples extending to different depths. Simulated-burrow probes were inside a 5 mm-diameter rigid, plastic tube (the width of an average *Seothyra* burrow) that was inserted into the sand. Temperature profiles of four burrows from which the spiders had been removed were compared with those of simulated burrows over 24-h periods.

(3) Thermal conductance along vertically and horizontally-oriented thermocouple wires. We compared the temperature profiles from burrows and simulated-burrow probes with those from thermocouples that were placed at the same depths, but laid horizontally for 10 cm from the terminal sensor to reduce the conductance of heat through the thermocouple.

### Thermal tolerance limits

We determined the temperatures at which spiders began showing behavioral signs of heat stress. Twenty-one newly captured spiders were measured and placed individually in plastic cups (52 mm diameter) which contained a shallow layer (5 mm) of dune sand. The spiders constructed surface mats and chambers, but were unable to dig vertical burrows. The cups containing the spiders were placed into direct sun in order to gradually heat up the sand. The rate of increase of surface temperature ( $t_s$ ) was  $3.5 \pm 1.7^{\circ} C \cdot \text{min}^{-1}$ . We recorded the  $t_s$  at which spiders moved vigorously (*thermal discomfort*) and at which they abandoned their chambers to erupt onto the surface (*thermal stress*). The latter is equivalent to the critical thermal maximum (CTM; Pulz 1987).

In addition, we determined the fate of spiders released on the surface of the sand at different ambient temperatures and tested whether spiders released at night were able to dig burrows of sufficient depth to survive the temperature regime the following day.

### Prey handling

Live prey were placed on the sticky silk of webs in the field to determine the influence of surface temperature on prey handling ability. We measured duration of the total sequence of prey capture and of the separate prey-handling bouts and interbouts (see below). We also noted the onset of weak struggling by the prey and the time at which struggling ceased altogether. Adult mealworms, *Tenebrio molitor* (Coleoptera, Tenebrionidae) ( $n=34$ ), and a natural prey species, the ant *Camponotus detritus* (Hymenoptera, Formicidae, Formicinae) ( $n=28$ ), were used as prey. The beetles were about four times the mass of the ants (beetles  $85 \pm 11$  mg,  $n=10$ ; ants  $24 \pm 12$  mg,  $n=50$ ). Sand surface temperature was measured near the end of each prey capture sequence.

We could infer the spider's presence in the surface chamber when we saw it at the entrance, from the presence of a bulge or movements in the chamber, from the restraint of a leg of struggling prey, or from shifting of immobilized prey being manipulated by the spider. At all other times the whereabouts of the spider remained unknown, but was assumed to be within the burrow.

We refer to segments of the prey capture sequence when the spider was either visible or inferred to be at the surface with the prey as *handling bouts*, and all other times when the spider could have been in the burrow as *interbouts*. Handling bout durations, thus defined, may have been underestimated if the spider was at the surface, but remained inconspicuous. Conversely, interbout durations may have been overestimated.

### Foraging activity

We examined the daily pattern of foraging activity of a sample of spiders in relation to temperature and wind regimes. We recorded the activity of spiders in the three study areas of Visnara at 4-h intervals over three separate periods of 24 h each, during

January 1988. Simultaneously, we monitored wind speeds and temperature profiles of burrows.

Webs of 100–225 spiders were recorded as open if the sticky edges of the surface mat were visible or closed if they were not, as was the case when the web was covered by wind-blown sand. The spider's latency of attack was the time taken between receiving a prey stimulus (simulated by lightly stroking the sticky silk with a fine brush) and the attack response. Spiders that did not attack within 15 s of the initial stimulus were recorded as not responding.

We used contingency tables to test the separate effects of sampling days, sample areas and the time of day on the opening of webs and on spider response. A three-way ANOVA was used to separate the influences of the same three factors on the latency of attack.

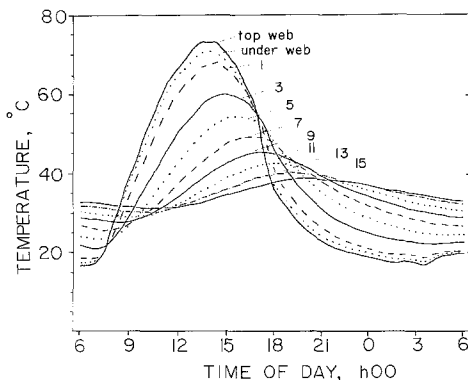
## Results

### *Thermal environment of the web*

Temperature profiles obtained using burrow probes, simulated burrows and loose thermocouples were similar in all cases ( $r=0.99$ ;  $P<0.01$ ). Near the surface, where the temperature gradient was steepest (Fig. 2), small differences in the placement of probes critically affected the readings (mean difference =  $0.5^\circ\text{C}$ ). As a result, the greatest divergence in temperatures recorded simultaneously from different probes ( $4.7^\circ\text{C}$ ) occurred near the surface of the sand during times of temperature extremes.

The presence of the surface mat had little effect on temperatures recorded beneath it or inside the burrow. The mean difference in temperature recorded on top of the mat and beneath it was  $0.3^\circ\text{C}$  (maximum difference =  $1.1^\circ\text{C}$ ). The principal difference occurred at night, when the sand beneath the mat cooled more slowly than the bare sand surface. These comparisons validated our use of simulated-burrow probes which we placed near occupied burrows to determine their temperature profiles over a range of environmental conditions.

The daily range of temperature was greatest at the surface and decreased with depth (Fig. 2). Surface temperatures often reached  $65\text{--}75^\circ\text{C}$  on sunny afternoons and experienced daily fluctuations of up to  $57^\circ\text{C}$ . However, below a depth of 12 cm, the daily range was less



**Fig. 2.** Temperature profiles obtained from a burrow probe placed at Visnara for 24 h on 6–7 January 1989. Thermocouples recorded temperatures on top of the mat, beneath the mat and at depths of 1, 3, 5, 7, 9, 11, 13, and 15 cm below the surface

than  $10^\circ\text{C}$  and the maximum temperature did not exceed  $41^\circ\text{C}$ . In the hot season, burrows usually exceeded this depth ( $13.3 \pm 1.6\text{ cm}$ ,  $n=198$ ). Burrow depth correlated poorly with spider size ( $r=0.33$ ,  $P<0.05$ ). Thus, the bottom of a *Seothyra* burrow is a relatively constant thermal environment, which rarely exceeds  $35^\circ\text{C}$ . By positioning themselves in various sites within the burrow, spiders may choose from a  $>30^\circ\text{C}$  range of temperatures at the hottest times of day.

### *Thermal tolerance limits*

Spiders tested in shallow cups in which they were only able to construct surface chambers, showed first signs of thermal discomfort at  $47.3 \pm 2.8^\circ\text{C}$  (range  $40.2\text{--}50.3^\circ\text{C}$ ). The critical thermal maximum (stress temperature) of  $49.0 \pm 2.0^\circ\text{C}$  (range  $42.9\text{--}51.4^\circ\text{C}$ ) was independent of spider body size (body length =  $3.2\text{--}8.2\text{ mm}$ ,  $P>0.1$ ) and was also independent of the rate of temperature increase ( $P>0.1$ ).

Spiders released on the sand at  $t_s < 46^\circ\text{C}$  built webs after a short period of searching and movement on the sand surface ( $2.5 \pm 1.33\text{ min}$ ,  $n=27$  spiders). Above this temperature, spiders sought shade beneath vegetation, or climbed up grass stalks where the temperature at 3 cm above the ground was about  $15^\circ\text{C}$  cooler than at the surface (mean difference:  $14.8 \pm 3.0^\circ\text{C}$ ,  $n=5$ ).

The minimum burrow depth necessary for *Seothyra* to maintain a body temperature below the average CTM of  $49^\circ\text{C}$  was calculated at  $5.7 \pm 0.54\text{ cm}$  ( $n=5$  simulated-burrow temperature profiles). When spiders were released on the sand in the early morning ( $n=4$ ), they built chambers immediately, but could not burrow deep enough to escape the increasing subsurface heat that killed them. We tested whether spiders that were released in the evening could dig burrows during a single night that were deeper than the predicted minimum depth. Burrow depth for these spiders was  $6.4 \pm 1.5\text{ cm}$  ( $n=69$  spiders) and was not correlated with spider size ( $P>0.05$ ). We calculated the maximum temperature endured by these spiders at the bottom of their burrows to be  $45.1 \pm 2.4^\circ\text{C}$ , using the temperature profile measured in a simulated burrow during the 24-h period following the release. Only one of the released spiders was found dead in a burrow 3.4 cm deep; the estimated maximum temperature at the bottom of this burrow was  $51.2^\circ\text{C}$ .

To assess long-term effects of different temperature regimes on fitness, we maintained spiders in captivity at  $35^\circ\text{C}$  and at  $25^\circ\text{C}$  ( $n=7$  at each temperature). Spiders kept at  $35^\circ\text{C}$  grew and reached maturity in less than eight months similar to those in the field, while those at  $25^\circ\text{C}$  grew more slowly and did not mature in one year.

### *Prey handling*

*Seothyra* was able to successfully attack and capture prey over the range of surface temperatures tested ( $16.7\text{--}68.8^\circ\text{C}$ ). Durations of handling bouts were similar for

**Table 1.** Comparison of durations of prey capture sequences with ants (*Camponotus detritus*) and beetles (*Tenebrio molitor*) as prey. For handling bouts and interbouts, means and standard errors are shown for the number (*n*) and the total, mean, maximum and minimum durations. Mean bout durations are means of the mean bout durations in all sequences. Mann-Whitney tests compare durations of sequences with ants (*n*=28) and beetles (*n*=34). \* = 0.01 < *P* < 0.05, \*\* = *P* < 0.001

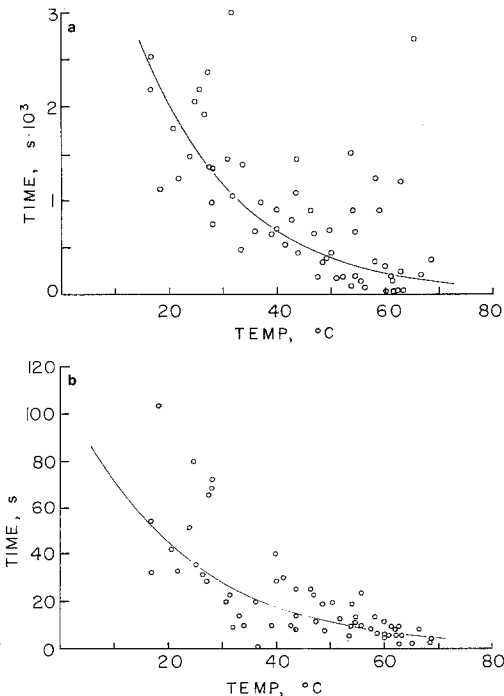
Behavior	Durations (min)			
	Ants		Beetles	
	Mean	SE	Mean	SE
Total sequence	17.9*	2.4	11.7*	2.0
Handling bouts				
<i>n</i>	7.1	1.1	6.8	1.2
Total	2.2	0.4	2.3	0.5
Mean	0.3	0.1	0.4	0.1
Max	0.8	0.2	0.7	0.1
Interbouts				
<i>n</i>	5.4	1.0	5.7	1.2
Total	12.9**	1.6	7.3**	1.2
Mean	6.4**	1.6	1.7**	0.3
Min	4.8**	1.7	0.6**	0.1

**Table 2.** A comparison of durations of capture sequences at  $t_s < 49^\circ\text{C}$  and at  $t_s \geq 49^\circ\text{C}$ . Shown are total capture sequence duration, total and mean handling bout durations and the number of handling bouts. Mann-Whitney tests are used to compare durations

Behavior	Durations (min)				Prob.
	<49° C		≥49° C		
	Mean	SE	Mean	SE	
Total sequence	20.16	2.01	7.96	1.81	<0.001
Handling bouts					
Total	3.08	0.52	1.23	0.24	<0.001
Mean	0.54	0.07	0.16	0.02	<0.001
Number	5.6	0.57	8.5	1.58	n.s.

correlated with surface temperature ( $r=0.66$ ,  $P<0.001$  for the total sequence), but was independent of the size of the spider. The durations of handling bouts (Fig. 3a, b), interbouts, maximum handling bouts and minimum interbouts decreased with increasing surface temperatures (all regressions are significant at  $P<0.05$ ). Maximum handling bout duration indicates how long a spider was able to remain at the surface. The minimum interbout duration represents the time spent in the burrow in order to avoid overheating at the surface. The extent to which prey continued to struggle in the web was inversely related to temperature ( $r=-0.49$ ,  $P<0.001$ ,  $n=44$ ). Thus, at  $t_s > 49^\circ\text{C}$ , insects succumbed more rapidly ( $2.6 \pm 1.8$  min,  $n=7$ ) and could be manipulated and pulled into the web more rapidly than at lower temperatures ( $11.1 \pm 9.5$  min,  $n=17$ ).

Capture sequence durations were significantly shorter above  $49^\circ\text{C}$  than below ( $P<0.001$  for ants and beetles combined; Table 2). The number of handling bouts in a capture sequence did not differ significantly ( $P>0.05$ ); thus, the difference can be attributed to shorter handling times at higher temperatures. Below  $35^\circ\text{C}$ , capture sequences were often very long (12 of 13 sequences lasted  $>15$  min). Spiders behaved lethargically and prey continued to struggle long after having been bitten. Long capture sequences ( $>15$  min,  $n=6$ ) occurred also  $\geq 49^\circ\text{C}$ , when spiders had difficulties pulling prey into the web because of prey size, incorrect orientation or because it was necessary to disentangle the insect from the sticky silk. In long capture sequences at  $\geq 49^\circ\text{C}$ , individual handling bouts were short ( $9.2 \pm 7.0$  s) and occurred at fairly regular intervals ( $46.4 \pm 23.3$  s).

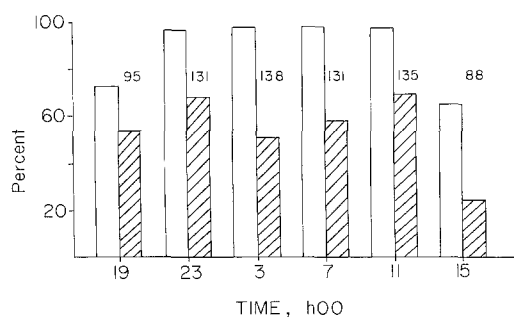


**Fig. 3a, b.** Durations (s) of ant and beetle capture sequences (combined) in relation to surface temperature ( $t_s$ ,  $^\circ\text{C}$ ): (a) total duration and (b) mean handling bout duration. The regression equations are: (a)  $e^{(8.7-0.05t_s)}$  ( $r^2=0.44$ ,  $P<0.001$ ,  $n=62$ ), (b)  $e^{(4.7-0.05t_s)}$  ( $r^2=0.52$ ,  $P<0.001$ ,  $n=62$ )

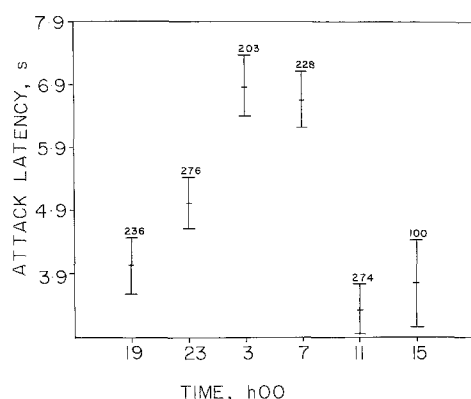
capture sequences with ants and beetles (Table 1). Therefore, we combined the data for ants and beetles for all analyses of handling-bout durations and of bout numbers. Prey capture duration was strongly negatively

### Foraging activity

We observed open *Seothyra* webs (i.e. with exposed sticky silk) at all sampling periods (Fig. 4). However, both the time of day and the sampling date influenced the number of webs that were closed (Table 3). Both effects were due to variable winds. During some afternoons, the wind speed increased to above  $1.8\text{ m}\cdot\text{s}^{-1}$  (measured at 20 cm height), which moved sufficient sand



**Fig. 4.** Activity of *Seothyra* at different times of day over three 24-h periods. Shown are the average percentages of open webs (clear bars) out of the total webs observed and the percentage of spiders responding to a prey stimulus (shaded bars) out of all individuals with open webs. The number of open webs at each time of day (averaged over 3 census days) is shown above the bars. Mean percentages were calculated from arcsin transformed data



**Fig. 5.** Mean attack latency (time in seconds to respond to a prey stimulus) for spiders at different times of day. Data from all days and census areas are combined. Vertical lines are 95% confidence intervals

**Table 3.** Summary of influences of time of day, sampling date and sampling area on *Seothyra* foraging activity. Web opening and attack response were tested with  $\chi^2$ , attack latency was tested by multifactor ANOVA. Degrees of freedom: time of day = 5, attack response = 2, area = 2

Behavior	$\chi^2$	Prob.
<b>Web opening</b>		
Time	446.6	<0.001
Date	445.9	<0.001
Area	5.7	n.s.
<b>Attack response</b>		
Time	142.9	0.001
Date	0.5	n.s.
Area	2.3	n.s.
<b>Attack latency</b>		
	F-ratio	Prob.
Time	39.2	<0.001
Date	1.9	n.s.
Area	2.0	n.s.

to cover the sticky silk and close many webs. Spiders in closed webs rarely responded to prey stimuli.

The tendency of spiders with open webs to respond by attacking when presented with a prey stimulus was influenced by the time of day (Fig. 4), but not by the sampling date nor area (Table 3). Only 24% of spiders with open webs responded by 1500h when surface temperatures were hottest (Fig. 2). High response tendencies in open webs (51–70%) were recorded at all other hours, when conditions were cooler. This suggests that very hot afternoon temperatures depressed the attack response of spiders, even though their webs remained open.

Attack latency also showed a clear pattern of variation with time of day (Fig. 5, Table 3). The spiders responded quickest at 1100 h, 1500 h and 1900 h compared to other times of day. The day and area of sampling had little effect on the reaction time of *Seothyra* to a prey stimulus (Table 3). The reaction time of spiders with open webs was thus fastest during times of day when the sand was hot (Fig. 5).

## Discussion

### *The thermal environment*

The bottom of the burrow of *Seothyra* provides a clement thermal environment. *Seothyra* burrows averaged 13 cm in depth in the hot season, irrespective of spider size. At this depth, the temperature fluctuated between 30–40° C, well below the temperature at which spiders began to show signs of thermal discomfort. Metabolic rates of seven *Seothyra* individuals were measured over 24 h periods at 30° C and 40° C. Resting metabolic rates were low at both temperatures (0.06 and 0.08 ml CO<sub>2</sub> · mg<sup>-1</sup>h<sup>-1</sup> at 30 and 40° C, respectively; J. Lighton, pers. comm., see Lighton et al. 1987 for techniques used). Thus, resting metabolic rate was relatively insensitive to temperature changes within this range ( $Q_{10}=1.57$ ,  $n=4$ ), suggesting that there was no thermal stress at 40° C (Moeur and Eriksen 1972).

Some burrowing spiders select a suitable thermal environment by using the temperature gradient within their burrows (Norgaard 1951; Humphreys 1974, 1978). Our observations indicate that *Seothyra* uses the burrow to maintain body temperature below the critical thermal maximum and that neither high midday temperatures nor low temperatures at night limit the spider's ability to forage. Signal strands enable *Seothyra* to detect prey at the surface from any position within the web. Short prey-handling bouts ( $\leq 10$  s) observed at high  $t_s$  suggest that the spider shuttles between the hot surface and the cool burrow during extended prey capture sequences.

### *Thermal tolerance*

*Seothyra* has possibly the highest critical thermal maximum (mean CTM = 49° C) of any spider species investigated (Pulz 1987). While methods of determining CTM

vary among investigators, it appears that other desert spiders have lower CTM's: 43° C for the burrowing mygalomorph, *Aphonopelma* sp. (Theraphosidae) (Seymour and Vinegar 1973) and <45° C for *Lycosa* (*Pardosa*) *carolinensis* (Lycosidae) in summer (Moeur and Erikson 1972). Both of these are primarily nocturnal.

High CTM's were recorded in actively-foraging diurnal arthropods, e.g. the Namib ants *C. detritus* and *Ocyrmymex barbiger* (Myrmicinae) (53 and 51.5° C, respectively; Curtis 1985b; Marsh 1985a), and some tenebrionid beetles (>47° C for 8 species of Namib tenebrionids, Hamilton 1975). *Seothyra* is a sit-and-wait predator living in a cool burrow; however, its temperature tolerance is more similar to that of active, diurnal desert foragers. Given its small size (body mass ≤300 mg for an adult *Seothyra*), a spider handling prey on the surface will heat up very quickly. Even allowing for cooling by shuttling into the burrow, a high CTM may be necessary if *Seothyra* is to forage during the hot hours of the day.

### Foraging strategy

Prey capture efficiency increases with ambient temperature. The increase is not linear, however, but exponential (Fig. 3), such that above approximately 40° C, the increment in efficiency decreases with further temperature increase. Above  $t_s = 49^\circ\text{C}$ , *Seothyra* must limit its forays to the surface. It does this by handling prey very rapidly, or by shuttling between the cool burrow and the surface to handle prey intermittently. In either case, we predict an increasing cost of foraging at higher temperatures as a result of increased rates of movement and/or greater distances moved.

Given the shape of the prey handling curve with respect to  $t_s$  and the increase in cost of foraging at higher temperatures, we predict that spiders will forage most efficiently at  $t_s = 40\text{--}49^\circ\text{C}$  and foraging activity will decline above 49° C. The observations of foraging activity in the population support this prediction qualitatively: at 1500 h (when  $t_s$  is near maximum) significantly fewer spiders responded to prey stimuli. The spiders that reacted to prey stimuli at this hour, responded very rapidly. Thus, while *Seothyra* may forage at all times of day, the cost of foraging increases at high temperatures and may influence the spider's decision to attack prey caught in the web.

There is an advantage of foraging during the hot hours of the day when ants such as *C. detritus* and *O. barbiger* are active on the surface. These long-legged ants are able to run rapidly across the sand and to take thermal refuge in clumps of vegetation (Curtis 1985a, 1985b, 1985c; Marsh 1985a, 1985b). *Seothyra* is one of very few predators (along with some antlions; Marsh 1987) able to capture ants during the time of day when they are maximally active (Marsh 1985b). At  $t_s \geq 49^\circ\text{C}$ , an average handling bout of 10 s was sufficient to attack and subdue most ants. A further advantage derives from the fact that insects trapped in the sticky silk are unable to escape boundary-layer conditions, where sand tem-

peratures may be 10–15° C hotter than the air only 5 mm above the surface (Curtis 1985a). Thus, the prey quickly succumbs to heat stress and is subdued rapidly. This may be particularly important for spiders handling large prey which otherwise may break the capture web and escape.

*Seothyra* reacted noticeably slower to prey stimuli and took longer to handle prey at  $t_s < 20^\circ\text{C}$  than at higher temperatures. This may put *Seothyra* at a disadvantage when foraging at night at a time when many arthropods are active on the surface (Crawford and Seely 1987). However, foraging activity remained high throughout the night. From 1800 h to 0800 h, the bottom of the burrow is actually warmer than the surface (Fig. 2). *Seothyra* may improve its foraging efficiency at night by using this inverted gradient to maintain a higher body temperature than that of the sand surface.

Two strategies of foraging in relation to temperature have been proposed for desert ectotherms: (1) Hamilton (1975) argued that many diurnally-active desert ectotherms (e.g. tenebrionid beetles) adopt a strategy of "maxithermy", i.e. they minimize the time spent at high body temperatures, primarily through behavioral thermoregulation. This strategy should enhance growth and reproduction, as the rates of both processes increase with increasing body temperature. Alternatively (2) nocturnal activity at relatively low body temperatures (Henwood 1975), may be more typical of desert burrowing arachnids (Main 1982; Cloudsley-Thompson 1982).

*Seothyra* fits neither of these categories. It remains active over the full range of ambient temperatures, as long as the sticky silk is not covered by wind-blown sand. A high CTM enables this spider to forage efficiently at high ambient temperatures, while maintaining body temperature below the stress level by shuttling between the hot surface and cool burrow. Foraging is also not restricted by low ambient temperatures: the sticky capture web restrains prey until the spider can attack and an inverse temperature gradient at night may enable the spider to warm up at the bottom of the burrow. As a result of these behaviors, *Seothyra* may forage during a period of 19–20 h per day. *Seothyra* is highly sedentary; long-term population monitoring in the Namib showed that burrows remained occupied continuously for many months (Henschel and Lubin, unpubl.). Given that *Seothyra* cannot alter its position with respect to potential prey, a "eurythermic" foraging strategy may be a response to generally low and/or unpredictable prey availability.

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