

Thermal constraints on prey-capture behavior of a burrowing spider in a hot environment

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Summary. *Seothyra henscheli* (Eresidae) is a burrowing spider that lives in the dune sea of the southern Namib Desert, Namibia. Prey capture by these spiders involves a foray from a cool subterranean retreat to the undersurface of a capture web that can be lethally hot. Striking, disentangling and retrieving prey from the capture web typically involves several short trips to the capture web, alternating with retreats to the cool burrow. It has been suggested that this behavior limits the increase of body temperature a spider must experience while working at the hot capture web. We used biophysical models in conjunction with direct observations of prey-capture behavior and distributions of sand temperature to estimate body temperatures experienced by *S. henscheli* during prey capture. In the circumstances we observed, only the relatively long post-strike retreat from the capture web is important in keeping spiders' body temperatures from exceeding their lethal limits. After the post-strike retreat, shuttling appreciably limits the increase in body temperature of small individuals, but may have little effect on body temperature increase in larger spiders.

Introduction

The soil surface of hot deserts is thermally one of the most extreme terrestrial environments (Louw and Seely 1982; Cloudsley-Thompson 1983). To survive here, an animal must either have extraordinary thermal tolerance, or have the means to avoid the most extreme temperatures that occur there. The latter option usually involves periodic retreat to a cool refuge, either in shade, or a few centimeters below the soil surface (Chappell

and Bartholomew 1981; Dreisig 1984; Schultz and Hadley 1987).

Avoiding extreme temperatures can mean suspending foraging or other important activities during the hottest parts of the day. This is the case for most burrowing arachnids, which limit activity to the cooler parts of the day (Riechert and Tracy 1975; Humphreys 1987; Cloudsley-Thompson 1962, 1983). An interesting exception to this may be found among certain burrowing spiders that inhabit the dunes of the southern Namib Desert, Namibia (*Seothyra henscheli*; Dippenaar-Schoemann 1990). These spiders' webs consist of a vertical silk-lined burrow that extends 10–15 cm below the surface of the dune, and a horizontal mat-like capture web on the surface of the sand. The edges of the mat are lined with sticky silk threads that trap small arthropods walking on the sand surface. When prey is entangled in the capture web, the spider ventures to the undersurface of the capture web to strike and subsequently disentangle the prey. During prey capture, although the spider is protected by the capture web from direct solar radiation, the temperatures underneath the web can approach 70° C (Lubin and Henschel 1990).

Although the burrow, where *S. henscheli* normally rests, provides a cool refuge, prey capture during the hottest part of the day involves a foray into a potentially lethal thermal environment. While disentangling and retrieving prey from the capture web, these spiders supposedly avoid overheating by (1) having an unusual tolerance to high body temperatures, with a critical thermal maximum (CTM) approaching 49° C (Lubin and Henschel 1990; Almquist 1970), and (2) by subduing and retrieving the prey in an episodic series of prey-handling bouts at the surface, "shuttling" between the hot capture web and the cool refuge of the burrow (Lubin and Henschel 1990).

In this paper, we examine whether the prey-capture behavior of *S. henscheli* represents "thermal shuttling", whereby the short visits to the hot capture web limit the increase of body temperature the spider must experience during prey capture. In order to answer this ques-

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tion, one must know the course of a spider's body temperatures during a prey capture episode, and what would happen to it if a particular behavior did not occur. The novel feature of our study is our use of a transient-state biophysical model to estimate the time course of spiders' body temperatures during prey capture. This model employs as inputs a spider's observed schedule of visits to, and retreats from, the capture web, combined with a measured distribution of temperatures within the web, and the spider's estimated rate of body temperature change. This approach also allows us to evaluate the effect of alternative prey-capture tactics on the time course of body temperature, and so to determine which behaviors were effective in limiting the increase in spiders' body temperatures.

Materials and methods

Study sites and species. This work was carried out at the Desert Ecological Research Unit (DERU) at Gobabeb, Namibia. Some aspects of the natural history, general ecology and structure of the web of this species, and study sites around the DERU at Gobabeb have been described by Lubin and Henschel (1990), and Henschel and Lubin (1992). The work reported here was done during the latter part of February 1989. Spider time constants (see below) were determined at the DERU laboratory at Gobabeb. Prey-capture behavior (see below) was observed at the Khommabes study site (*sensu* Lubin and Henschel 1990), a vegetated traverse dune located about 5 km NW of Gobabeb (23°33'S; 14°49'E).

Spider time constants. The rate of change of a spider's body temperature is quantified by the time constant, τ (s). Time constants were determined for spiders *in situ* (1) underneath the edge of a capture web, (2) at the entrance to the burrow covered by the capture web, and (3) at several depths within the burrow itself. Additionally, time constants were determined for spiders in shade and in still air.

Four spiders ranging in body mass from 30.6 to 154.6 mg (mean = 72.7 mg \pm 49.2 mg/SD) were prepared for time constant measurements as follows. A spider was induced to come to the edge of the capture web, where it was captured and then killed with ethyl acetate. In the laboratory, a 40-Ga type T thermocouple was implanted into the spider's body, and the wound sealed with a drop of cyanoacrylate adhesive. The spider's corpse was mounted on the tip of a small wooden sting. The spider was spray-painted with a thin layer of flat black lacquer to facilitate measurement of the time constant in the burrow, because bristles on an unpainted body would frequently snag on the silk lining the burrow, destroying it. We found that painting the body did not affect its time constant.

Time constants (τ) were determined from body temperature transients of the mounted spiders, using the method of Bakken (1976). Cooling time constants in still air were measured in a closed room at the DERU in Gobabeb. This provides an appropriate comparison with spiders in burrows, where neither wind nor direct solar radiation affect the spider's heat balance. The spider's body was heated with a heat lamp. When body temperature was about 45° C, the lamp was switched off. As the body cooled, the time course of its body temperature was noted, and the time constant calculated from this.

Time constants within burrows were measured during a hot sunny day, in a patch of riverine sand that contained many webs of *S. henscheli*. Between measurements, the mounted spiders were kept cool in an insulated box. First, we located an occupied web of *S. henscheli*. The spider residing therein was captured and placed aside in a plastic vial. If possible, the spider was returned later

to its web. The edge of the vacated capture web was then gently lifted and a mounted spider corpse was placed either under the edge of the capture web, under the capture web at the burrow entrance, or into the burrow at some measured depth. The spider's temperatures were then recorded as it warmed, and the time constant determined from these temperatures. After the experiment the corpse was returned to the insulated box and allowed to cool until it was used again. If inserting the spider into the burrow destroyed the web, data from this determination were not used.

Sand temperature and prey-capture behavior. Prey-capture behavior and burrow temperatures at several *S. henscheli* webs were observed during 14–17 February 1989. A field-capable data-logging system, comprising a portable microcomputer (Radio Shack TRS-80 Model 100, Dallas, TX) coupled to a multiplexed A/D converter (Remote Measurement Systems ADC-1, Seattle, WA) was used to simultaneously record (1) prey-capture behaviors, (2) times at which the behaviors occurred and (3) sand temperature profiles adjacent to the web. Sand temperature profiles were measured using probes made according to the specifications of Lubin and Henschel (1990), which measured sand temperatures at 0, -1, -3, -5, -7 and -9 cm from the sand surface.

Sixty prey-capture episodes were observed by two of the authors (JST and YDL). An active web was located and the temperature profile probe was sunk into the sand adjacent to the web. A prey item, usually a captured worker ant (*Camponotus detritus*), was then placed on the capture web; this was recorded on the data-logger as the start of the prey-capture episode. The time at which the spider struck the prey was recorded, as was the time the spider withdrew from the capture web. Each time thereafter the spider visited the capture web, this was recorded on the data-logger, as well as each time the spider left the capture web, apparently to retreat into the burrow. The time at which the spider finally recovered the prey and hauled it into its burrow was recorded as the end of the prey-capture episode. If, within 15 min, the spider had either not struck, or had not recovered the prey, the observations were terminated, and these data were not used in subsequent analyses. Once observations of the prey capture episode were completed for the web, it was marked, and another web was selected for the next set of observations.

Each time a behavioral observation was recorded, the computer also recorded the web's temperature profile. These temperatures were averaged over time for the prey-capture episode to give an average vertical temperature distribution in the burrow during the prey-capture episode.

From the time sequences of behavior, we estimated: (1) the *time to strike* as the time between placement of the prey, and the first appearance of the spider at the capture web, (2) the *post-strike retreat* as the time between the end of the spider's first visit (when the prey was presumably envenomed), and the beginning of the spider's second visit (when retrieval of the prey commenced), (3) the *capture time* as the elapsed time between placement of the prey and the spider's recovery of the prey from the capture web, (4) the *subjugation time* as the time for the strike and the post-strike retreat, corresponding roughly to the time required for the prey to succumb and become manageable, (5) the *retrieval time* as the time required for the spider to bring the prey into the burrow once it has succumbed, (6) the *handling time* as the total time spent by the spider at the capture web during the post-retreat visits (Fig. 1).

After all observations were completed, each web observed was dug up and the spider residing therein captured. Lengths of the capture webs (± 1 mm), lengths of the burrows (± 1 mm) and the masses of the resident spiders (± 0.1 mg) were measured.

Estimated spider temperatures during prey capture. To estimate the course of a spider's body temperature during prey capture, terms are required for: time constant of the spider, times at and away from the capture web, temperature of the capture web, and temperature at the spider's retreat in the burrow. Details of how these estimates were made are provided in Appendix 1.

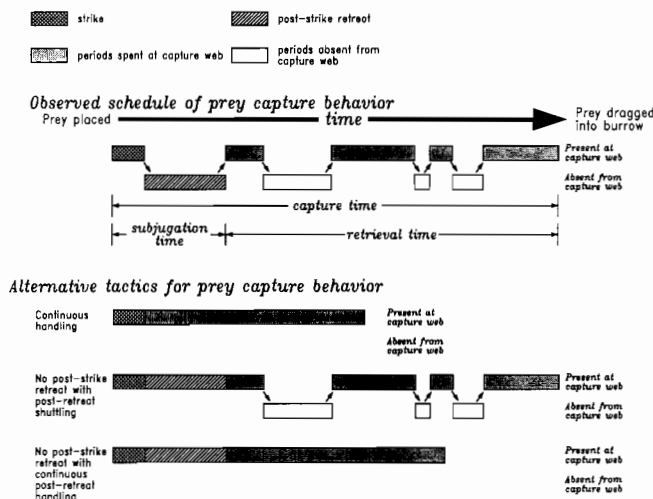


Fig. 1. Time lines describing the time course of prey capture by *Seothyra henscheli* and associated subsidiary times. In addition, three alternative tactics for the time lines used to calculate body temperatures during a prey-capture sequence are given. These are: *continuous handling*, in which every interval the spider was observed to spend at the surface is condensed to form a continuous visit to the capture web; *no post-strike retreat with post-retreat shuttling*, in which the spider is assumed to stay with the prey during the normal post-strike retreat, followed by intermittent visits to the capture web that follow the observed schedule of visits; and *no post-strike retreat with continuous post-retreat handling*, in which the spider spends the post-strike retreat with the prey, and condenses all the observed post-retreat visits into a single post-retreat visit that is continuous with the post-strike retreat

The time constant of a particular spider was estimated from its body mass, using the empirical relationship between body mass and τ (see below). The time and surface temperature terms were measured directly during the prey-capture episodes. Measurement of temperature at the retreat was complicated by our ignorance of where in the burrow the spider retreated to. We therefore used the measured temperature profile to derive a polynomial equation relating depth to sand temperature. We then assumed retreat depths of -3 cm, -5 cm and -7 cm, and performed separate analyses for each. (Because of technical problems with one of the probes, we could not reliably estimate burrow temperatures for retreat depths greater than -7 cm.)

Alternative prey-capture tactics. To evaluate the putative benefit of shuttling behavior, we estimated the maximum body temperature a spider would attain for four tactics describing a prey capture episode. Details of how these estimates were made are provided in Appendix I.

The tactics, schematized in Fig. 1, are:

1. Maximum body temperature if the spider had followed the observed schedule of visits to and retreats from the capture web, designated $T_{\max,sh}$
2. Maximum body temperature if the spider stayed at the capture web for a single continuous visit of duration equal to the total time the spider was observed to be at the capture web, designated $T_{\max,c}$
3. The maximum body temperature if the spider had stayed with its prey during the post-strike retreat, followed by the observed schedule of visits to and retreats from the capture web, designated $T_{\max,nr}$
4. The maximum body temperature if the spider had stayed with its prey during the post-strike retreat, followed by a continuous visit to the capture web of duration equal to the total time the spider was observed to be at the capture web, designated $T_{\max,nrc}$

Results

Spider time constants

In still air, spiders' time constants were on average 75% longer than they were under the capture web (Fig. 2). Body mass of the spider had a clear and significant effect on the time constant (Fig. 2), both in still air ($r^2 = 0.9998$), and under the edge of the capture web ($r^2 = 0.979$). The time constants were not significantly affected by location of the spider in the burrow, down to depths of -10 cm ($r^2 = 0.0579$; $n = 18$).

Prey-capture behavior

A capture sequence typically involved: (1) a strike within a few seconds of placing the prey onto the capture web, followed by (2) a post-strike retreat from the capture web while the prey died, followed by (3) one or more

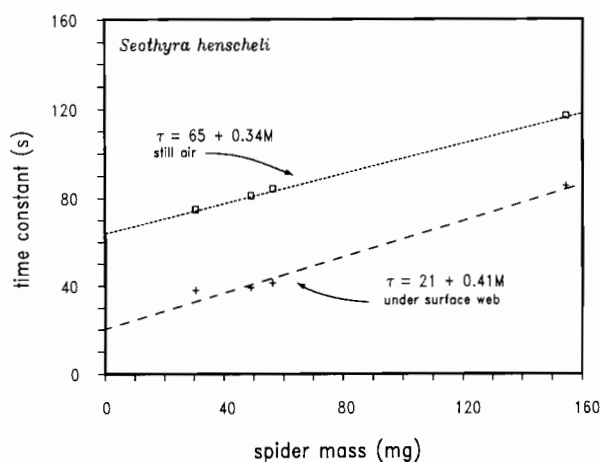


Fig. 2. Time constants for four Namib *Seothyra henscheli*, measured in still air (squares) and under a capture web (crosses). Lines represent least-squares best fits for spiders in still air (dotted line) and spiders under a capture web (dashed and dotted line)

Table 1. Characteristics of prey-capture episodes for *Seothyra henscheli*. Numbers are median (quartile)

	Median (± 1 quartile)	Maximum/ minimum
Time to strike (s)	4 (3–10)	57 2
Average duration of visits to capture web (s)	9.0 (5.3–14.5)	161.5 2.5
Duration of post-strike retreat (s)	118 (26–196)	1011 3
Handling time (s)	27 (18–43)	323 5
Capture time (s)	153 (60–238)	1032 11
Time constant (s)	41.2 (30.1–49.9)	91.0 15.1

post-retreat visits of the capture web to disentangle the prey from the silk and drag it into the burrow (Fig. 1).

Of the active spiders 75% struck within 10 s of the prey being placed on the capture web (Table 1). The median post-strike retreat length was about 2 min, but these were highly variable among spiders, with 25% of the post-strike retreats ranging roughly from 3 to 16 min (Table 1).

Nearly all spiders disentangled and retrieved the prey with four or fewer post-retreat visits to the capture web (Fig. 3). Spiders most commonly paid two post-retreat visits to the capture web – one visit to begin disentangling the prey from the capture web, and a second visit to complete the job and retrieve the prey. Nevertheless, nearly a third of the spiders disentangled and retrieved the prey in only one post-retreat visit. Three spiders had to visit the web ten or more times to retrieve the prey. In four cases, the spider struck, but did not retrieve the prey within 15 min.

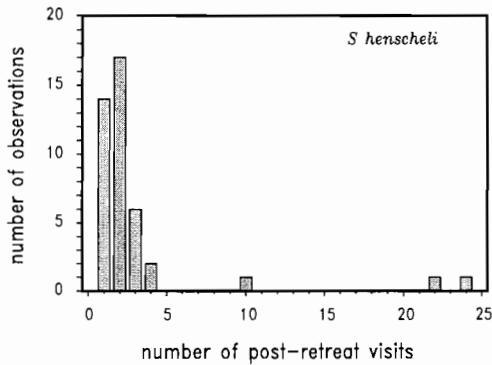


Fig. 3. Number of post-retreat visits to the capture web required to disentangle and retrieve the prey

Post-retreat visits to the capture web were commonly very brief – 75% were 15 s or less (Table 1). The median capture time was about 4 min, of which the spider spent about one-sixth actually handling the prey (Table 1).

Sand and burrow temperatures

Sand temperature profiles showed a typical pattern of high temperatures and variability at the surface, and moderating and damping of temperatures at depth (Fig. 4).

Temperatures at the surface ranged from about 20° C in the morning, and peaked at about 55–60° C by 1400 hours (Fig. 4). Sand surface temperatures exceeded these spiders' critical thermal maximum (CTM: 49° C) by 1000–1130 hours. At a depth of –3 cm, some of the sand temperatures exceeded the spiders' CTM by 1400 hours, commonly by less than 1° C. At depths of –5 cm and below, temperatures never exceeded CTM.

Characteristics of webs and spiders

Spiders observed during prey-capture episodes weighed on average about 71 mg (Table 2), resulting in an average time constant of about 50 s. Burrows averaged about 15 cm in depth, with the shallowest about 10 cm deep (Table 2).

Estimated spider temperatures during prey capture

There were 37 prey-capture sequences that were suitable for estimating maximum body temperatures. Of these,

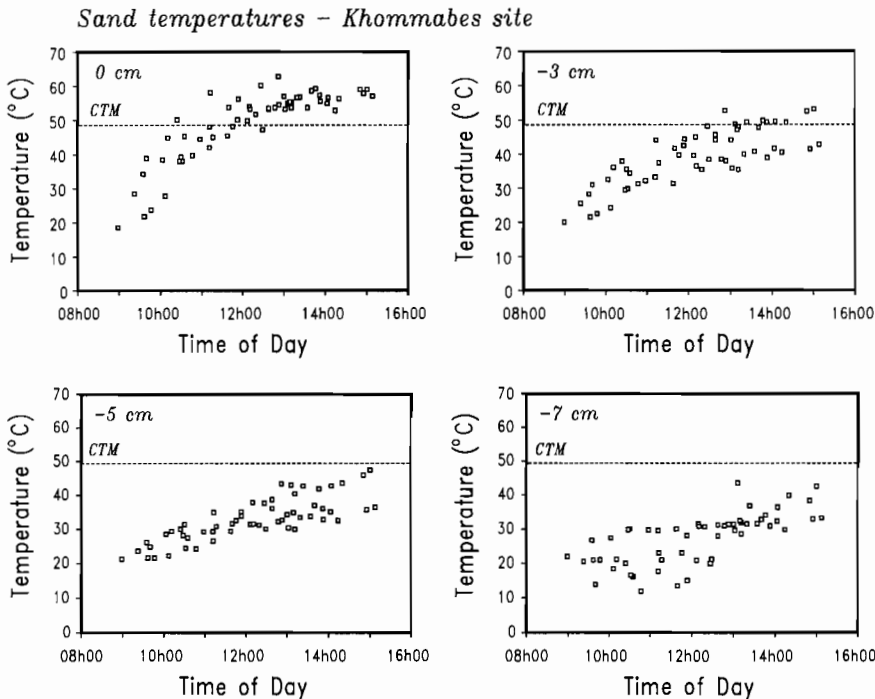


Fig. 4. Sand temperatures during observed prey-capture episodes. Each *point* represents the average temperature at the depth indicated for an individual spider's web. Depth of temperature measurement is indicated in the *upper left corner* of each panel. *CTM*: critical thermal maximum (°C)

Table 2. Characteristics of webs and spiders from the Khommabes site

	Average	SD	Maximum	Minimum
Width of capture web (mm)	60.8	20.7	112	27
Depth of burrow (mm)	147.3	25.1	230	101
Body mass (mg)	70.8	36.5	167	42

20 had surface temperatures exceeding the CTM of 49° C. Among all spiders, the observed schedule of shuttling behavior kept maximum body temperatures well below 49° C (Table 3). Among the spiders that visited capture webs warmer than 49° C, the observed schedule of shuttling behavior always resulted in the least number of spiders exceeding the CTM, irrespective of retreat depth (Table 4). At an assumed retreat depth of -7 cm, only one spider would have experienced a lethal body temperature (Table 4). The shallower the retreat depth, the lower was the number of spiders that could successfully capture prey without exceeding the CTM (Table 4).

Of the alternative prey capture tactics, those that forced the spider to spend the post-strike retreat at the

Table 3. Estimated maximum body temperatures attained during alternative prey-capture tactics outlined in Fig. 1

Prey capture tactic	Retreat depth (cm)		
	$d = -3$	$d = -5$	$d = -7$
Observed schedule	42.5 (8.0)	39.0 (7.1)	37.4 (6.6)
Continuous prey-handling	43.2 (8.2)	40.2 (7.8)	38.7 (7.5)
No post-strike retreat with observed post-retreat shuttling	46.3 (9.1)	45.0 (9.3)	44.4 (9.4)
No post-strike retreat with continuous post-retreat prey-handling	46.5 (9.2)	45.4 (9.3)	44.9 (9.4)

Maximum body temperatures for the different tactics were estimated using the equations outlined in Appendix I. Numbers are mean (SD)

capture web would have had the most deleterious effect on body temperature (Tables 3, 4). Because the post-strike retreats are generally long with respect to the spiders' time constants (Table 1), forcing a spider to spend this time at the hot capture web effectively forces

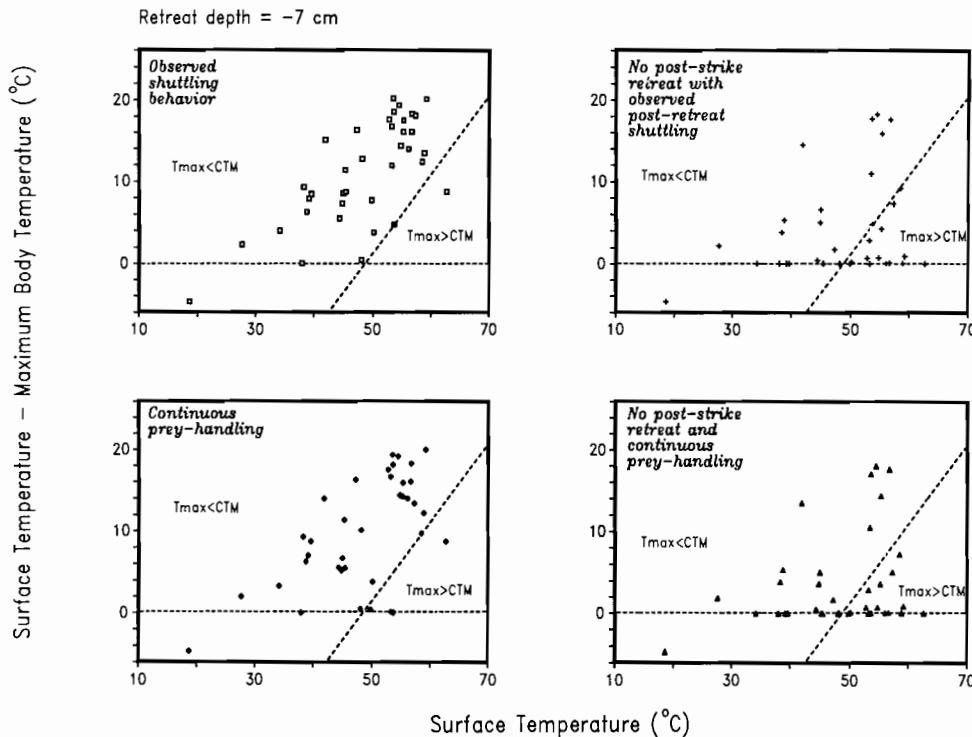


Fig. 5. Thermal consequences of shuttling behavior at an assumed retreat depth of -7 cm. Plots are of the temperature difference between calculated maximum body temperature for each of four behavioral tactics, and surface temperature of the associated web, i.e. how effectively the spider kept its body temperature below surface temperature. *Diagonal dotted line* indicates where the calculated body temperature equals the CTM, and so divides the plot into two domains: to the *left*, where body temperature stayed below

CTM, and to the *right*, where body temperature exceeded CTM. The *horizontal line* indicates where body temperature equals the temperature at the capture web. The four behavioral tactics are those described in Fig. 1. *Top left*, observed schedule of shuttling behavior; *lower left*, continuous prey-handling; *top right*, no post-strike retreat with observed post-retreat shuttling; *lower right*, no post-strike retreat with continuous post-retreat prey-handling

Table 4. Proportion of prey-capture bouts in which both surface temperature and estimated body temperature exceeded 49° C

Prey capture tactic	Retreat depth (cm)		
	$d = -3$	$d = -5$	$d = -7$
Observed schedule	0.400	0.150	0.050
Continuous prey-handling	0.550	0.300	0.200
No post-strike retreat with observed post-retreat shuttling	0.850	0.750	0.700
No post-strike retreat with continuous post-retreat prey-handling	0.900	0.750	0.750

Body temperatures were estimated from prey-capture tactics outlined in Fig. 1

its body temperature to approach surface temperature (Fig. 5). The post-strike visits, on the other hand, are short compared to the spiders' time constants. Whether taken separately or lumped together (Table 1). Consequently, even if the handling time had been spent in a single continuous visit, most spiders could have captured prey without exceeding the CTM (Tables 3 and 4; Fig. 5).

Discussion

If an ectotherm ventures into a lethally hot environment, its body temperature will eventually equilibrate to the environmental temperature, and the ectotherm will die. However, an ectotherm's body temperature does not change instantaneously, but with a time delay, owing to the animal's "thermal inertia". An ectotherm should therefore be able to venture into a lethally hot environment with no ill effects, provided the duration of the foray is short enough. Specifically, if an ectotherm making a foray into a hot environment allows its body temperature to rise until it reaches a threshold temperature, T_{th} , the duration of the foray, t_{foray} , will be:

$$t_{foray} = -\tau \ln [(T_{th} - T_{eq}) / (T_0 - T_{eq})] \quad (1)$$

where τ = thermal time constant, T_{th} = the threshold temperature as defined above, T_{eq} = the environmental temperature of the unfavorable environment, and T_0 = body temperature at the start of the foray. If a single foray into the hot environment is not sufficiently long to find, subdue and retrieve a prey, an animal can make repeated forays into the hot environment, intermittently retreating to a cooler environment to cool down preparatory to the next foray. This type of behavior is known as thermal shuttling.

There are good grounds for inferring that *S. henschei*'s prey capture behavior is thermal shuttling. *S. henschei* will capture prey even when the capture webs' temperatures far exceed the spiders' lethal temperatures.

These spiders retreat from the prey immediately after a strike, and frequently must make several short visits to the capture web to retrieve the prey. These behaviors are apparently unusual: most web-building spiders, including those in the family Eresidae, do not abandon the prey immediately after a strike or during prey retrieval, but stay with the stricken prey until it succumbs and is secured (Norgaard 1941; Robinson 1975). Finally, *S. henschei*'s small body size, and commensurably short thermal time constant, τ (Table 1) limits the duration of any foray to the capture web (Eq. 1). The circumstantial case that *S. henschei*'s prey capture behavior is thermal shuttling is therefore a strong one.

However, for *S. henschei*'s unusual prey-capture behavior truly to be considered thermal shuttling, two additional criteria should be met. First, the observed schedule of shuttling should limit the increase of body temperature a spider experiences during prey capture. Second, altering the prey-capture behavior, so that the purported thermal shuttling behavior is absent or altered in some critical way, should result in a larger, and deleterious, increase of the spider's body temperature.

It would appear from our estimates that the first of these criteria is met. For the observed schedule of visits to the capture web, the spiders' estimated body temperatures usually stayed well below the temperature of the capture web (Fig. 5). Because the durations of the post-retreat visits were usually short, roughly 25% of the thermal time constant (Table 1), the spider was rarely at the capture web long enough to thermally equilibrate with it (Fig. 5). If the retreat was sufficiently deep (and cool), estimated body temperatures for nearly all spiders could have been kept lower than the CTM of 49° C (Table 4; Fig. 5).

Evaluating the second criterion is more difficult. We did so by calculating what effect certain alternative prey capture tactics would have on a spider's maximum body temperature. In constructing these alternative tactics, we were guided by two assumptions. First, we assumed that the aggregate time to strike, subdue and retrieve a prey for a particular spider-ant encounter is fixed by circumstances such as prey body size, spider body size and degree of entanglement of the prey (and hence difficulty of disentanglement). We are presuming that this total time will be fixed, whether the task of prey capture is undertaken in one continuous bout at the capture web, or is split up into several intermittent bouts. Second, we assumed that the two unusual aspects of *S. henschei*'s prey-capture behavior, namely the post-strike retreat and the post-retreat shuttling, could be treated independently.

Based on these assumptions, three alternative sets of prey-capture tactics were constructed, and their consequences for body temperature during prey capture were assessed (Fig. 1). To test the effect of the post-retreat shuttling only, we allowed the spider its normal post-strike retreat but compressed all the post-retreat handling into a single continuous bout. To test the effect of the post-strike retreat only, we allowed the spider to carry out its normal schedule of post-retreat shuttling, but kept the spider at the capture web after the strike

until it began to retrieve the prey. To test the effect of both together, we eliminated the post-strike retreat, and compressed all the post-retreat handling into a single continuous bout.

Prey capture tactics that only eliminated the post-retreat shuttling appeared to have little consequence for spiders' body temperatures during prey capture. If spiders spent their handling times in a continuous bout at the capture web, estimated body temperatures still would have stayed well below temperature of the capture web (Table 3; Fig. 5), and most spiders' body temperatures would not have exceeded CTM (Table 4; Fig. 5).

The reasons for this are straightforward. The post-retreat visits to the capture web were usually less than 10 s each (Table 1), and four such visits were most commonly required to disentangle and retrieve prey: in many cases, only one post-retreat trip to the web was sufficient (Fig. 3). Consequently, the spiders' total times at the capture web still were generally shorter than their thermal time constants (Table 1). It appears, therefore, that the post-retreat shuttling behavior does not meet the second criterion for thermal shuttling, and should not be so considered.

Very small spiders proved to be an obvious exception to this. For most of the prey-capture sequences observed, there was no evident relationship between the number of visits to the capture web, and either temperature of the capture web or body mass (Fig. 6). However, three spiders (designated S18, S33 and L19; Table 5) paid an exceptionally large number of post-retreat visits to a lethally hot capture web (Fig. 6). These were the same

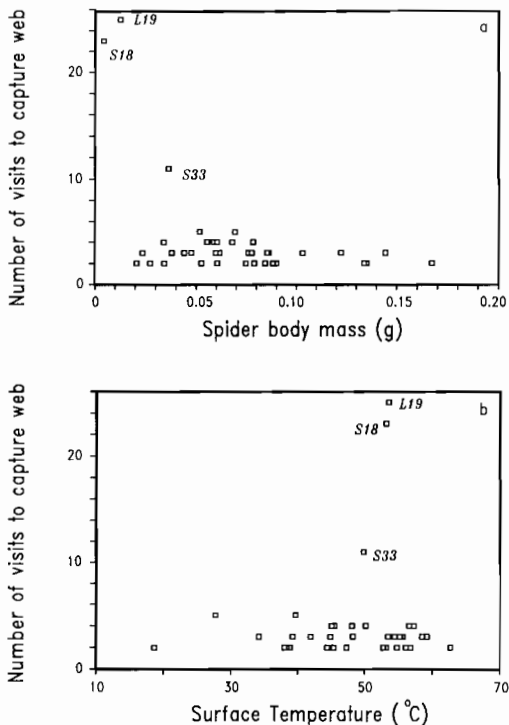


Fig. 6a, b. Number of visits to the capture web for all observed prey capture episodes against **a** body mass of the spider, and **b** temperature of the surface web. Points with alphanumeric designations correspond to the individual spiders described in Table 5

Table 5. Characteristics of spiders, prey capture episodes and calculated maximum body temperatures for the three small spiders discussed in the text

Spider	S18	S33	L19
No. of visits	23	11	25
Body mass (mg)	4.2	36.4	12.5
τ (s)	15.1	30.1	19.0
Handling time (s)	77.0	120.0	131.0
T_s ($^{\circ}\text{C}$)	53.2	49.9	53.6
$T_{\text{max,sh}}$ ($^{\circ}\text{C}$)	38.9	41.6	48.9
$T_{\text{max,c}}$ ($^{\circ}\text{C}$)	53.1	49.5	53.6
$T_{\text{max,nr}}$ ($^{\circ}\text{C}$)	53.2	49.9	48.9
$T_{\text{max,nrc}}$ ($^{\circ}\text{C}$)	53.2	49.9	53.6

Retreat temperature is assumed to be the lowest measured temperature consistent with the depth of the burrow, i.e. the coolest refuge the spider could have sought

spiders whose maximum body temperatures were calculated to exceed or closely approach the CTM, even with the observed schedule of post-retreat shuttling (Fig. 5). Because these three spiders' handling times exceeded their time constants by 4–7 times (Table 5), not allowing them to engage in post-retreat shuttling would have forced their body temperatures to equilibrate with the hot capture web, with fatal consequences (Table 5).

The post-strike retreat, in contrast, does appear to meet the second criterion for thermal shuttling. The post-strike retreat is considerably longer than the spiders' time constants: if this time is spent at the capture web, equivalent to the usual habit of a spider staying with a stricken prey until it dies, the calculated body temperatures of many spiders thermally equilibrate with the capture web (Table 3; Fig. 5). Consequently, when surface temperatures exceed the CTM, many spiders' body temperatures would have exceeded the lethal limit (Table 4). This was true whether or not the spider shuttled during the post-retreat handling phase: if the post-strike retreat had not been taken, nearly all would have fatally overheated (Table 4).

We conclude, therefore, that the post-strike retreat of *S. henscheli* is a true example of a thermal shuttling behavior. The post-retreat shuttling behavior, in contrast, is not.

Our conclusions must be tempered by a few qualifications. First, the environmental conditions in our study were not the most extreme that these spiders experience. The surface temperatures during our study usually were in the mid- and upper-50 s $^{\circ}\text{C}$ (Fig. 4). However, the hottest months in the Namib typically are March and April, and surface temperatures at this time can approach 70 $^{\circ}\text{C}$ (Lubin and Henschel 1990). The post-retreat shuttling might have kept even adult spiders from overheating under these more extreme thermal regimes. Nevertheless, that post-retreat shuttling occurs even when it is not thermally necessary, as was the case in our study, suggests that whatever thermal benefits might accrue are coincidental to some other reason for the behavior.

We also have assumed that the principal benefit to a shuttling spider is the avoidance of lethally hot body

temperature. This may be unrealistically strict, however, because benefits can accrue at body temperatures lower than the critical thermal maximum. For example, while prey capture by tiger beetles (*Cicindela hybrida*) is most efficient at highest tolerable body temperatures, prey availability in their habitats falls off sharply at high temperatures (Dreisig 1981). Consequently, the “best” body temperature for maximizing prey capture *rate* is cooler than the “best” body temperature for maximizing prey capture *efficiency* (Dreisig 1981). Presumably, natural selection would “set” the regulated body temperature, and hence the threshold temperature for leaving a hot microenvironment, to this optimal temperature.

Whether such considerations apply to *S. henscheli* is unknown. As in tiger beetles, prey capture by *S. henscheli* is most efficient at temperatures close to the CTM (Lubin and Henschel 1990). However, unlike the foraging tiger beetle, which must balance the likelihood of finding prey against the likelihood of subduing it, *S. henscheli* is essentially a “sit-and-wait” predator, one that will only engage a prey when it stumbles into the web. Thus, the factors that optimize tiger beetles’ foraging temperatures to a cooler temperature than the CTM, may not apply to *S. henscheli*, i.e. there is good reason to believe that *S. henscheli* will be a maxitherm (Hamilton 1973).

Both these qualifications should be balanced against the conservative assumptions we made for retreat depth into the burrow. These spiders will not survive the day if their burrows are shallower than 5 cm (Lubin and Henschel 1990). Our assumptions of retreat depth bracketed this critical depth. Although we do not know where in the burrow the spider retreated to, the average depths of the burrows make it possible for the spiders to have retreated deeper than this (Table 2). For those circumstances where time at the surface was less than or similar to the spiders’ time constants, the estimated maximum temperatures could have been cooler.

With the thermal consequences of the unusual prey-capture behavior of *S. henscheli* clarified, it is interesting to ask how these behaviors benefit the spider and how any accrued benefits balance against any associated costs. In the case of the post-strike retreat, the benefits are clear – the spider is far less likely to lethally overheat. The costs also seem evident: in several cases, we noted that the ant would escape the capture web after being struck. Once this happens, of course, it is impossible for the spider to recover the prey. Perhaps abandoning the prey after the strike forces *S. henscheli* to forgo injecting a venom load sufficient to ensure a successful capture.

In the case of the post-retreat shuttling, the costs and benefits are less clear. There is little reason to suppose that the post-retreat shuttling contributes much to keeping body temperatures from overheating, except for very small spiders handling apparently unwieldy prey. The costs are also not clear. Leaving the prey at the surface for a longer period desiccates the prey, and makes it more likely that a surface-dwelling scavenger, like a bird, might spot the stricken prey and steal it. It would seem, therefore, to make little sense for the behavior to be

maintained. Why it obviously is retained is unknown to us.

In summary, burrowing spiders (*S. henscheli*) that inhabit the hot dunes of the Namib desert often make forays into a hostile thermal environment to capture prey. When these spiders capture prey, they engage in a series of visits to the capture web, involving a strike, a post-strike retreat into a cool burrow, and a series of short visits to the capture web to disentangle and retrieve the prey. The intermittent post-retreat visits do not appear to be crucial in limiting the increase in body temperature a spider experiences during its forays to the hot capture web. The principal exception seems to be for very small spiders handling relatively large and unwieldy prey. However, the post-strike retreat from the capture web does appear to be crucial in keeping the spiders’ body temperatures within their vital limits.

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Appendix I

Estimating spider temperatures during prey capture. Each time the spider changes location in its burrow, its body temperature will change. The exact temperature change will depend upon, (1) the spider’s time constant, τ , (2) what the spider’s body temperature was when it changed location, (3) what equilibrium temperature the spider would eventually reach if it remained at its new location, and (4) how long the spider spends at the new location before it moves again.

Assuming the body temperature is a first-order transient (Turner 1987), its course can be estimated by the following formula:

$$T_t = (T_0 - T_{eq}) \exp(-t/\tau) + T_{eq} \quad (I-1)$$

where T_t = body temperature at time t , T_0 = temperature at the beginning of the transient, T_{eq} = equilibrium temperature (which T_t will approach if t is very long), and τ = time constant for temperature change (s). This formula estimates both warming and cooling temperatures.

A shuttling spider will move back and forth between the hot capture web at the surface and the cooler burrow. A single shuttling bout will occupy the time from when a spider becomes visible at the web, through the time the spider retreats, until the time the spider becomes visible again. At this time, the next shuttling bout will start. It shuttling bouts are numbered sequentially, bout 1 will go from $t_{v,1}$ to $t_{v,2}$, or more generally, bout n will occur between $t_{v,n}$ to $t_{v,n+1}$. At some time during bout n , the spider will disappear from the capture web, at time $t_{u,n}$ (Fig. I-1).

When the spider arrives at the capture web, its temperature will rise toward the surface temperature, T_s . What temperature it actually attains, $T_{n,w}$, will depend upon how long it spends there, which, for bout n , is $t_{u,n} - t_{v,n}$, and upon what the spider’s body temperature is when it arrives at the surface (Fig. I-1). When the spider leaves the capture web at time $t_{u,n}$, its body temperature will cool toward the burrow temperature at the depth it rests at, T_d (Fig. I-1). What body temperature actually is reached, $T_{n+1,c}$, how long it spends in its burrow before venturing back to the capture web, which, for, for bout n , is $t_{v,n+1} - t_{u,n}$, and upon

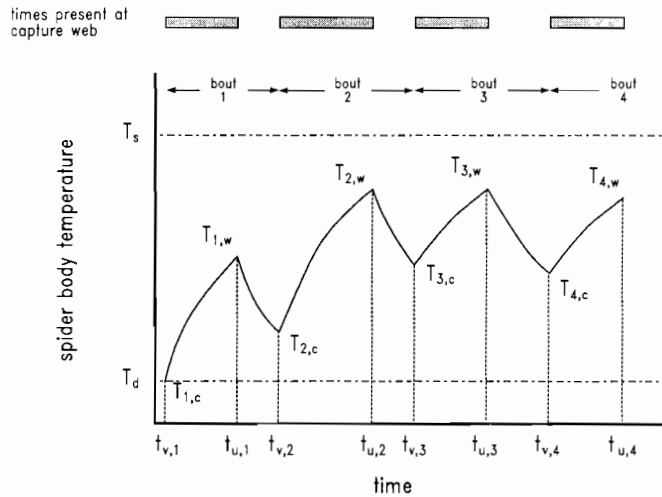


Fig. I-1. Schematic diagram explaining terminology of temperatures and shuttling behavior. Each shuttle bout consists of a time at the web (*shaded bar*) and a time not at the web (*unshaded interval*). For shuttle bout n , the spider appears at the capture web at time $t_{v,n}$, and remains until it disappears, at time $t_{u,n}$. During this time the spider's temperature rises from $T_{n,c}$ to $T_{n,w}$. The shuttle bout n ends when the spider reappears at the web, at time $t_{v,n+1}$, which of course starts shuttle bout $n+1$. During this period, the spider's temperature declines from $T_{n,w}$ to $T_{n+1,c}$.

what the spider's body temperature was when it retreated, or $T_{n,w}$ (Fig. I-1). This will begin the next shuttle bout.

With these things and Eq. I-1 in mind, we can write equations describing the alternating temperatures during a prey-capture sequence. After placing the prey, the spider arrives at the capture web at time $t_{v,1}$. Until it retreats at time $t_{u,1}$, the spider's temperature rises to:

$$T_{1,w} = (T_d - T_s) \exp [(t_{v,1} - t_{u,1})/\tau] + T_s \quad (I-2a)$$

When the spider retreats, its temperature will decline to $T_{2,c}$, which is calculated:

$$T_{2,c} = (T_{1,w} - T_d) \exp [(t_{u,1} - t_{v,2})/\tau] + T_d \quad (I-2b)$$

Subsequent temperatures during shuttling are calculated by:

$$T_{n,w} = (T_{n,c} - T_s) \exp [(t_{v,n} - t_{u,n})/\tau] + T_s \quad (I-3a)$$

and

$$T_{n,c} = (T_{n-1,w} - T_d) \exp [(t_{u,n-1} - t_{v,n})/\tau] + T_d \quad (I-3b)$$

The maximum temperature attained during this tactic, $T_{\max,sh}$, is simply the maximum of the list of temperatures $\{T_{1,w}, \dots, T_{n,w}\}$.

Alternative prey-capture tactic: Continuous handling. This tactic assumes that all times at the surface are combined into a single continuous bout, of duration equal to the total time the spider was observed to spend at the surface. The maximum body temperature for a spider engaged in this type of behavior, $T_{\max,c}$, is simply:

$$T_{\max,c} = (T_d - T_s) \exp [\text{SUM}(t_{v,n} - t_{u,n})/\tau] + T_s \quad (I-4)$$

Alternative prey-capture tactic: No post-strike retreat followed by post-retreat shuttling. This tactic assumes that the post-strike retreat, which always has duration $t_{v,2} - t_{u,1}$ is spent at the surface. Thus, the first visit to the web combines the strike, post-strike retreat and first post-retreat visit into a single continuous visit. The duration of the first visit is therefore $t_{u,2} - t_{v,1}$. The temperature reached during this visit is therefore:

$$T_{w,1} = (T_d - T_s) \exp [(t_{v,1} - t_{u,2})/\tau] + T_s \quad (I-5a)$$

During the first retreat, the spider will cool to:

$$T_{c,1} = (T_{w,1} - T_d) \exp [(t_{u,2} - t_{v,3})/\tau] + T_{w,1} \quad (I-5b)$$

For the remainder of the visits, the temperatures attained are:

$$T_{w,n} = (T_{c,n-1} - T_s) \exp [(t_{v,n+1} - t_{u,n+1})/\tau] + T_s \quad (I-6a)$$

and during the remainder of the retreats, the spider will cool to:

$$T_{c,n} = (T_{w,n} - T_d) \exp [(t_{u,n+1} - t_{v,n+2})/\tau] + T_{w,n} \quad (I-6b)$$

The maximum temperature attained during this tactic, $T_{\max,nrc}$, is simply the maximum of the list of temperatures $\{T_{1,w}, \dots, T_{n,w}\}$.

Alternative prey-capture tactic: No post-strike retreat followed by continuous handling. This tactic assumes that the time spent at the surface includes the combined durations of the observed visits plus the post-strike retreat. The maximum body temperature for a spider engaged in this type of behavior, $T_{\max,nrc}$, is simply:

$$T_{\max,nrc} = (T_d - T_s) \exp [(t_{u,1} - t_{v,2} + \text{SUM}(t_{v,n} - t_{u,n})/\tau] + T_s \quad (I-7)$$

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