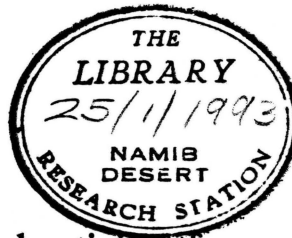


10146

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Environmental factors affecting the web and activity of a psammophilous spider in the Namib Desert

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For web-building spiders, shifting sand dunes would seem an inhospitable habitat. Nonetheless, one species of web-building spider *Seothyra henscheli* (Eresidae) is locally abundant in the Namib Desert dunes. Here we describe the structure of the web and examine the influence of certain environmental factors on web design and spider activity. Wind-blown sand covers the web's capture elements and disrupts foraging activity. Webs in wind-exposed areas are subject to greater sand-loading and/or scouring than in sheltered areas. Variation among habitats in web size may be explained by differences in local wind regimes: webs in wind-exposed sites have smaller capture elements than those in sheltered sites. Construction of a new web and web repair following disturbance are energetically expensive and expose the spider to risks of predation, overheating and desiccation. Environmental constraints on foraging and the cost of web-building help to explain the seasonal pattern of activity of *S. henscheli*.

Introduction

Spiders spin silken structures for protection and to forage. Such structures are considered to be webs if some components are snares which are employed in the detection and capture of prey (Foelix, 1982; Shear, 1986a). Webs often incorporate both retreats and snares. Retreats, if present, are used for shelter and concealment and are usually tubular in shape. Snares are often situated on frame threads that space out adhesive silk and signal strands for foraging purposes (Foelix, 1982; Nentwig & Heimer, 1987).

In desert dunes, spiders must contend with climatic extremes and with the physical properties of sand (Chew, 1961; Cloudsley-Thompson, 1983; Henschel, 1990a; Seely, 1991). The properties of dune sand that may influence web design and spider behaviour include its particulate nature, mobility, the paucity of vegetation, and a microclimatic gradient with depth. Dune-dwelling spiders in the Namib Desert avoid above-ground conditions by retreating into silk-lined burrows (Henschel, 1990a, b; Lubin & Henschel, 1991) or by sand-swimming (pers. obs.). Few species in this region use webs; most are wandering spiders.

Web spiders usually require firm surfaces to anchor their frame threads (Janetos, 1986). Furthermore, maintaining adhesive capture silk may be problematic in conditions of wind-blown sand. To understand the advantages, limitations and consequences of building webs in the dunes, we focus on the only obligatorily psammophilous web spider

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10146

of the central Namib Desert dunes, the eresid *Seothyra henscheli* (Dippenaar). This cribellate spider places its capture threads along the edges of a horizontal silk mat on the sand surface and uses a burrow as its retreat.

In a study of foraging behaviour at thermal extremes, Lubin & Henschel (1991) found that *S. henscheli* needs to burrow deep enough into the sand (>5 cm) to escape temperatures higher than its critical thermal maximum (49°C). Furthermore, foraging appeared to be restricted not only by high sand-surface temperatures (>65°C), but also by wind. In spite of these apparent limitations, *S. henscheli* is very common in the dunes, occurring in densities of up to 50 webs m⁻², and evidently has no web-building competitors. Here we explore some of the abiotic factors that affect the web structure and foraging behaviour of *S. henscheli*.

Sand temperatures and local wind patterns in the Namib Desert vary markedly with season (Lancaster *et al.*, 1984; Lancaster, 1989). We address the hypothesis that abiotic factors that affect spider activity on a daily basis (Lubin & Henschel, 1991) also explain differences in web design and foraging activity among habitats and between seasons. Consequently, we (1) describe the web and web-building behaviours of *S. henscheli*, and the web's function in foraging and in protection from adverse climate and predators, and (2) assess the influence of abiotic factors on web design and foraging activity by means of experimental manipulations and comparisons among habitats and seasons.

Study areas

Two principal dune study areas were situated at Visnara (1 km south of Gobabeb: 23°34'S, 15°02'E) and at Khommabes (6 km west of Gobabeb: 23°33'S, 14°49'E). The former site comprised low dunes adjacent to trees along the Kuiseb River and the latter a valley between linear dunes. Vegetation at both sites was sparse, with grasses (<1% cover) interspersed with clumps of *Acanthosicyos horridus* (Cucurbitaceae). A third study area was on a sandy terrace of the Kuiseb River bed. The site was a relatively wind-sheltered clearing (80 × 40 m), devoid of vegetation, but bordered by trees. All sites contained a diverse fauna of arthropods (Crawford & Seely, 1987), including at least 25 species of sand-dwelling spiders.

Additional data on the distribution and web sites of *S. henscheli* were obtained during visits to 28 different sites in the central Namib between 23–24°S and 14–16°E. These included sandy areas at inselbergs, in the Kuiseb River bed and in the Namib dune sea.

Methods

A study of *S. henscheli* was carried out at Visnara over 2 years. In three areas of 200 m² each, webs were monitored weekly during 1988 and at 2–4 week intervals in 1989. For each web, we determined if the spider was present and active. Sample sizes at Visnara were 195–616 webs in 1988 and 616–1144 in 1989. Webs that showed no signs of activity for >5 months, were assumed to be abandoned from 1 week after activity was last recorded. One of the 200 m² areas was subdivided into 1 m² quadrats. To determine if spider density correlated with the duration of exposure to direct solar radiation, we recorded for each quadrat whether it was predominantly (>50%) in the sun or shade. Observations were made at hourly intervals on a clear, midsummer day.

To compare the distribution of spiders among different habitats, we surveyed webs at Khommabes during March 1988. We counted all webs found on five 4 m wide transect lines (each 1.8 km in length) which included six dune habitats: slipface, upper plinth, lower plinth, dune base, interdune vegetation hummocks and interdune gravel plain.

We determined the size distribution of spiders at 2 month intervals at the three main

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10101

study sites. At each site, eight non-contiguous sample blocks of 10 × 10 m were selected randomly each time. We excavated and measured all *S. henscheli* webs found in one morning's search, captured the spiders and collected the remains of prey found in the burrows. The spiders were sexed, measured (with callipers or ocular micrometer, ±0.1 mm) and weighed (±0.1 mg) in the laboratory and released in the evening at their original web site.

Spiders that were used for experiments were removed from dune sites outside the three principal study areas. In the laboratory, spiders were kept in buckets filled with sand to a depth of 15 cm and were fed mealworm larvae (*Tenebrio molitor*) *ad libitum*. The rate of CO₂ production was measured hourly in six juvenile *S. henscheli* (39–87 mg) over 24 h in dark chambers at 40°C (Lighton, pers. comm.; following methods described in Lighton *et al.*, 1987).

To examine the cost in terms of spider mass loss upon construction of new webs, we excavated 15 spiders (range of body sizes 5–150 mg), measured their mass and burrow depth and released them in the evening. This was repeated seven times with the same spiders at 3–4 day intervals over a period of 23 days. For the first four releases, the experiment was carried out on open dune sand, and thereafter in closed buckets filled with sand and kept outdoors. Spiders were fed houseflies 1 day before the experiment, but were not fed during the experiment. Data for spiders ($n = 3$) that captured prey during the experiment were excluded from the analysis for the next stage. Three spiders escaped within the first three releases and were eliminated from further analyses.

The effects of wind-blown sand on webs of *S. henscheli* were examined as follows. We monitored 16 large webs (web length >5 cm) in an exposed dune area during one afternoon as wind speed increased gradually. At 10 min intervals, we recorded whether the web was exposed, partly covered or completely covered by wind-blown sand. Wind speed was recorded during three 1 min intervals at the start of each reading, using a wind totaliser (model Lambrecht, Göttingen) placed 18 mm above the sand surface. We converted wind totaliser measurements to wind speed at 1 m height using Geiger's equation (Geiger, 1973) with a ground coefficient of 0.25 in order to compare them with published values.

To assess the effects of wind on spider activity throughout the day, we monitored webs in three areas at Visnara characterised by differing degrees of exposure to wind. Fifty webs in each area were checked at 4 h intervals over three separate 24 h periods and wind speeds were measured using wind totalisers placed in the centres of each of the three areas.

Effects of sand accumulation on webs were tested on 20 webs over 14 days during summer in each of the three areas at Visnara (above) differing in their degree of exposure to wind. To exaggerate wind-blown sand accumulation, we heaped one tablespoon of sand onto each experimental web (10 in each area) in the early evening, after the afternoon winds had abated. Each morning, we examined the webs for activity, and sand was added in the evening to webs which showed activity in the morning. In addition, at the start and end of the experiment, we measured the height of the sand layer (measured against a thin wire rod inserted to a known depth at the edge of each web) and other web variables. In each area, 10 unmanipulated webs served as controls.

Data on meteorological conditions at Gobabeb on hourly, daily and annual time-scales were obtained from the Desert Ecological Research Unit. Wind-caused potential sand flow (Q) on a flat sand dune was calculated (in tonnes m⁻¹ h⁻¹) using the equation (Bagnold, 1953)

$$Q = 1.0 \times 10^{-4} (\log_{10} 100z)^{-3} (U - U_t)^3 T$$

where T is the time period over which wind speed of U was recorded (1 h), U_t the threshold wind speed that moves sand (16 km h⁻¹), z the height at which wind speed was measured (2.5 m).

Wind-induced changes in sand surface levels were monitored in Visnara by measuring it along small stakes (plastic knives) placed at the corners of 1 m² grid squares. Data for each square was the mean of its four corners.

Throughout the paper, means are given \pm one standard error. Statistical tests follow Sokal & Rohlf (1981).

Results

Natural history

The genus *Seothyra* is limited to sandy, semi-arid to arid regions of southern Africa (Dippenaar, 1991). The known distribution of *S. henscheli* is the southern Namib dune sea and adjoining sandy areas, but it has not been found in the cold, windy, crescentic dunes which extend from the coast to 20 km inland (Besler, 1972).

Webs were found in substrata ranging from the coarse sand of interdune plains to fine, loose silt of a dry river bed. In a cross-habitat survey at Khommabes, the proportions of spiders in various habitats differed significantly from the proportions of surface area covered by each habitat ($\chi^2 = 116$, df. = 5, $p < 0.001$). Most of the spiders (83% of 325 webs) were on exposed, low-lying sandy areas between dune vegetation hummocks. This habitat covered 34% of the study area. Some (16%) occurred on interdune plains and dune bases (covering 48% of the area). Only rarely (1%) were webs found on the lower dune plinth and none on the upper plinth and slipface (23% of the area). Similarly, 79.4% of the spiders ($n = 107$) that we collected in other areas were found on gentle dune slopes.

Seothyra henscheli characteristically occurred in colonies. High-density patches (five to 50 spiders m^{-2}) extended over *c.* 10 m^2 and were surrounded by larger areas ($\pm 50 m^2$) of lower density (0.5–5 spiders m^{-2}). Few spiders were found away from colonies.

Adult *S. henscheli* are sexually dimorphic. Males are brightly coloured and are smaller than females (mass 49 ± 10 vs. 108 ± 6 mg, $t = 3.4$, $p < 0.005$, body length 8.5 ± 0.5 vs. 9.4 ± 0.2 mm, $t = 1.9$, $p < 0.01$). During the mating season (May–July), adult males were caught in pitfall traps ($n = 5$) and were observed walking on the sand surface by day for periods of up to 1 h ($n = 12$). Near Gobabeb, males closely resemble the dune ant *Camponotus detritus*; elsewhere they resemble the ant *C. fulvipilosus* or mutillid wasp *Dasylabris* sp. Although abundant, the acid-spraying *Camponotus* ants are aggressive and not preferred as prey by potential predators such as lizards *Merops cuneirostris* (Murray & Schramm, 1987). Similarly, stinging mutillid wasps may be avoided by predators. We suggest that male *S. henscheli* derive protection on the surface from Batesian mimicry of noxious insects.

We found adults only in winter; females in April–September, males in May–July. Females tended egg cocoons ($n = 6$ observations) in August and nurseries from August to October ($n = 8$). Juveniles dispersed to dig new burrows in September–November. Laboratory spiders maintained at 35°C reached adulthood in their first year ($n = 30$). In the field, however, not all spiders matured in their first winter. At Visnara, 14% of the 1988 population ($n = 195$) and 6% of the 1989 population ($n = 616$) survived the winter as immatures, foraged during the following summer and matured in their second winter.

Web structure and function

The web of *Seothyra* comprises a horizontal chamber on the sand surface and a vertical, silk-lined burrow (Peters, in press; Fig. 1). The chamber is a shallow, elongated depression in the sand covered with a silken roof. The chamber roof or surface mat is usually covered with sand and has several lobe-shaped extensions which open into pits. The lobes are edged with sticky capture silk. The top of the burrow is joined to the chamber roof on one side and the burrow rim forms a collar door that can be pulled inward by the spider to close the entrance.

The walls of the burrow and surface mat are made of closely interwoven silk that binds

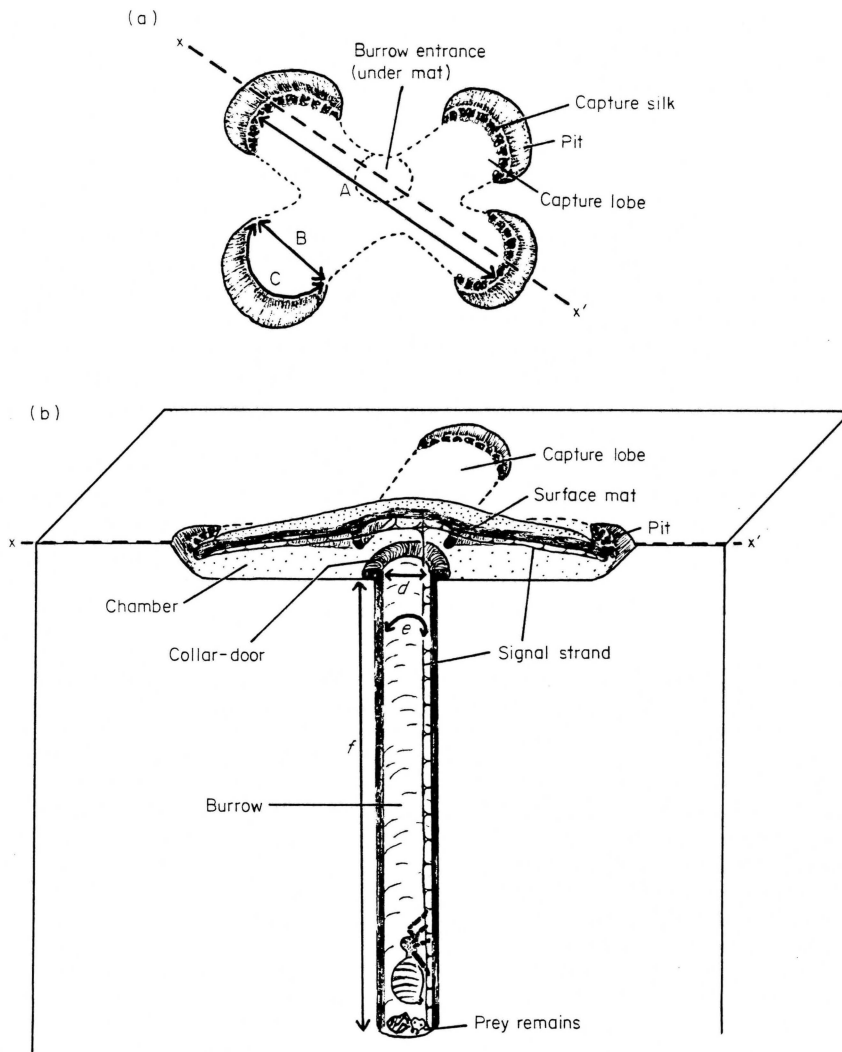


Figure 1. Web of *S. henscheli*. Schematic diagrams showing (a) top view of the surface mat *in situ* with open capture lobes and (b) vertical cross section through the web at X-x'. Web variables measured or estimated were: A, mat length; B, capture lobe width; C, capture silk length; D, diameter of the burrow entrance; E, half burrow circumference; F, burrow depth.

surrounding sand. With time, silk is added to thicken the surface mat and to lengthen the lobes. Fresh cribellar capture silk is regularly laid onto the distal edges of the lobes. This silk adheres to insect cuticles and is highly elastic. Multi-strand threads span the underside of the mat, leading from the lobes to the bottom of the burrow. These strands are loosely attached to the inside walls of the chamber and burrow and appear to have a signalling function, alerting the spider to the presence of prey trapped on the capture lobes.

The web of *S. henscheli* acts as a trap for small, terrestrial arthropods. The arthropod slips into the pit at the edge of a capture lobe where it becomes stuck in the cribellar silk and is attacked by the spider from beneath the mat. Ants were the main prey, constituting 87% ($n = 1441$ prey items) of the spider's diet in the dune habitats and 56% ($n = 1927$ items) in the river bed.

The web may protect the spider against many predators and parasitoids. Pompilid

wasps are known parasitoids of other burrowing dune spiders (Henschel, 1990b), but apparently do not attack *S. henscheli*. We have evidence for nine predators of *S. henscheli*, some of which are also kleptoparasites (Table 1).

Web size correlates

Body length and mass were highly correlated ($r^2 = 0.96$; Table 2), but as body length was easier to measure in the field than was mass, it was used throughout. Web parameters measured were: maximum length of the surface mat, widths of capture lobes, diameter of the burrow entrance, burrow circumference and burrow depth (Fig. 1). The length of sticky edges on each lobe (capture silk length) correlated well with lobe width (capture silk length = $0.17 + 1.37 \times$ lobe width; $r^2 = 0.91$, $n = 70$ lobes, range of widths 6–27 mm). Therefore, this relationship could be used to calculate the total length of silk available for capturing prey.

Burrow circumference, burrow entrance diameter, lobe width and the length of the surface mat were all significantly correlated with body length at all study sites (Table 2). Burrow depth was only weakly correlated with spider length and most (80%) of the burrows were 10–15 cm deep. The length of capture silk was not dependent on spider size,

Table 1. Predators and kleptoparasites of *S. henscheli*. Instances where a behaviour was inferred from indirect observations are shown in parentheses

Species	Type	Activity	Site	<i>n</i>
<i>Mirafra erythrochlamys</i> (Dune lark)	K (P)	D	M (S)	3
<i>Meroles cuneirostris</i> (Lizard)	K (P)	D	M (S)	4
<i>Gerbillurus paebe</i> & <i>G. tytonis</i> (Gerbils)	P	N	B	16
<i>Galerella sanguinea</i> (Slender mongoose)	P	D	B	3
<i>Leucorchestris arenicola</i> (Heteropodid spider)	K (P)	N	M	8
<i>Palpimanus</i> sp. (Palpimanid spider)	P	D?	B	8
<i>Asemesthes lineatus</i> (Gnaphosid spider)	P	D	S	3
Myrmeleontidae (Antlion)	P	N	S	1

Type: P, predator; K, kleptoparasite. Activity: D, diurnal; N, nocturnal. Site: B, burrow; M, mat; S, sand surface. *n*, number of observations.

Table 2. Spider and web morphometric variables for *S. henscheli* measured at three study sites combined (Visnara, Khommabes and Kuiseb River bed). The proportion of the variation explained by spider body length (r^2 , $p < 0.001$) is shown for each variable

Variable	Mean \pm S.E.	Range	<i>n</i>	r^2
Body length (mm)	5.3 \pm 0.1	2–13	460	
Body mass (mg)	27.9 \pm 1.6	1–239	451	0.96
Burrow circumference (mm)	13.1 \pm 0.2	4–38	791	0.77
Average lobe width (mm)	9.6 \pm 0.2	2–22	754	0.75
Mat length (mm)	37.2 \pm 0.8	6–148	811	0.64
Capture silk (mm)	36.7 \pm 0.8	6–128	788	0.48
Burrow depth (mm)	124.8 \pm 0.9	55–265	758	0.36

n, sample size.

but correlated rather with the number of capture lobes (Spearman rank $r_s = 0.51$, $p < 0.001$).

Building behaviour

When a spider was released onto the sand, it walked slowly for a short stretch, then stopped and attached silk to the sand surface with its extended anterior spinnerets to construct a small, oval mat. The spider then flipped onto its back and crawled beneath the mat.

Thereafter it added silk to the mat and constructed a silk-lined burrow. Capture threads were sometimes laid at the edges of the mat on the first night. Irrespective of body size, spiders burrowed down to 6.4 ± 1.5 cm ($n = 69$) in the first night and to 10.3 ± 1.7 cm ($n = 36$) by the third night. The surface mat remained small and oval in shape, but its length was correlated with spider length ($r^2 = 0.76$, $p < 0.01$). Over the first 4 weeks after release, spiders continued to lengthen the mat by an average of 4.9 ± 0.6 mm or 11% per week (ANOVA $F = 29.74$, $p < 0.001$, $n = 50$ spiders of body length 8.2 ± 0.2 mm). There was no significant increase in mat length during the following 2 weeks.

To determine if spiders varied their pattern of search for web sites in relation to habitat or to the type of substratum, we released spiders at dusk in three different habitats simultaneously: dune hummocks ($n = 21$), dune plinth ($n = 23$) and interdune plain ($n = 25$). The substratum of the first two habitats was dune sand and the latter was fine gravel with dune sand. Neither the time spent on the surface nor the distance moved varied with habitat (Kruskal-Wallis $p > 0.05$). However, in all habitats, spiders moved shorter distances as it got darker (Spearman rank, $r_s = -0.35$, $p = 0.003$).

Maintenance behaviour

Web maintenance activities took place daily after winds had covered the webs with sand, and at less frequent intervals when the burrow and surface mat were lengthened. After a wind, the spider flicked the edge of the capture lobes to dislodge the sand. Apparently, the spherical, wind-polished grains of dune sand do not adhere to the cribellar silk threads, and the capture lobes retain their stickiness. New cribellar silk was sometimes added to the lobes. When a spider outgrew the burrow, it built a new one contiguous with the old one, continuing to use and extend the original chamber and surface mat. Sometimes the entire web was abandoned and the spider shifted to a new site. Of 994 webs monitored at Visnara during 1988 and 1989, 18% were new webs of relocated spiders.

Construction work on the burrow and deposition of sticky silk were carried out at night. When kept in the laboratory without sand, spiders showed restless behaviour and had elevated metabolic rates in the evening and at night, corresponding to the time of web repair. Mean hourly metabolic rates ($n = 6$ spiders) were low during the morning and early afternoon (0.13 – 0.20 $\mu\text{l CO}_2 \text{ mg}^{-1} \text{ h}^{-1}$) and increased during late afternoon to midnight (0.25 – 0.46 $\mu\text{l CO}_2 \text{ mg}^{-1} \text{ h}^{-1}$).

Web relocation

The cost of relocation and web-building was estimated in terms of mass loss by forcing 15 spiders to dig several new burrows over a short time-span. There was a steady decline in body mass over the 23 days of the experiment of $6.5 \pm 0.4\%$ for each new web built. The rate of decline was only weakly correlated with spider size ($r^2 = 0.16$) and with the duration

of the experiment ($r^2 = 0.07$). At the end of the experiment, spiders had lost $30.4 \pm 2.3\%$ of their initial body mass.

Spiders built shorter burrows after successive releases ($r^2 = 0.74$, $p < 0.001$; Fig. 2) irrespective of their initial body mass. Following their fourth release, burrows were usually shorter than 55 mm, the minimum depth required to avoid exceeding the spider's critical thermal maximum (Lubin & Henschel, 1991). In the field, most spiders would have died of heat stress at this stage. In sheltered buckets, the spiders continued to build successively smaller webs, but failed to build at all on six occasions after day 13. One spider died on day 20, another on day 23 and four more ignored food presented to them after the experiment and died on day 27.

The greatest risk of web relocation may be that of predation on the surface. Nonetheless, we observed only four instances of predation on the surface in >100 release events (Table 1). Spiders that were released on the surface in the evening began constructing a small mat within 48.5 ± 5 s, moving 0.3 ± 0.05 m from the release point ($n = 72$). Construction of the preliminary mat took 73 ± 8 s; thus, the total time spent exposed on the surface was usually <3 min.

Thermal conditions

In summer, the surface mats of unshaded webs reached maximum temperatures of 55–75°C that far exceeded the spider's critical thermal maximum (Lubin & Henschel, 1991). At Visnara, we found significant variation in the density of webs in relation to the duration of solar radiation to which they were exposed. The minimum duration of exposure to direct sun of any web on a clear day was 6 h. The density of webs was significantly greater ($t = 4.48$, $p < 0.001$) in 55 quadrats that were in the sun for <8 h (4.7 ± 1.0 spiders m^{-2}) than in 91 quadrats that received 8–14 h of sun (1.1 ± 0.2 spiders m^{-2}). Although the densities were higher in shaded areas, no webs were seen directly beneath trees.

There is considerable seasonal variation in sand temperature, even at 5 cm depth. The

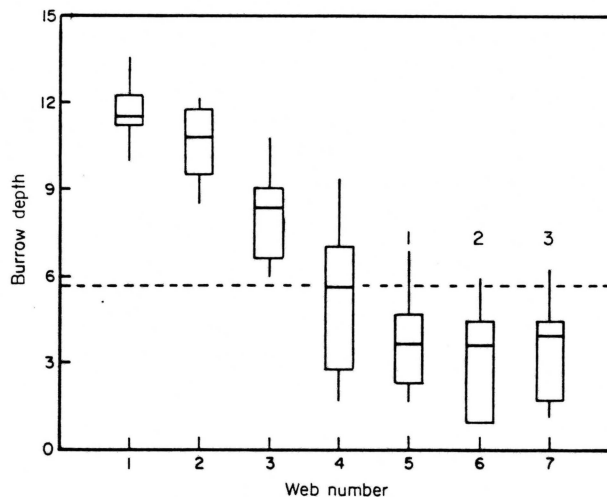


Figure 2. Cost of web-building. Lengths of successive burrows constructed over a period of 23 days by spiders that were removed from their webs and released to build new webs. Medians (horizontal lines), upper and lower quartiles (bars) and range (vertical lines) are shown. The numbers of spiders that did not build new webs are shown above the bars for webs 5, 6, and 7. The dashed line indicates the depth at which field temperatures exceeded CTMax.

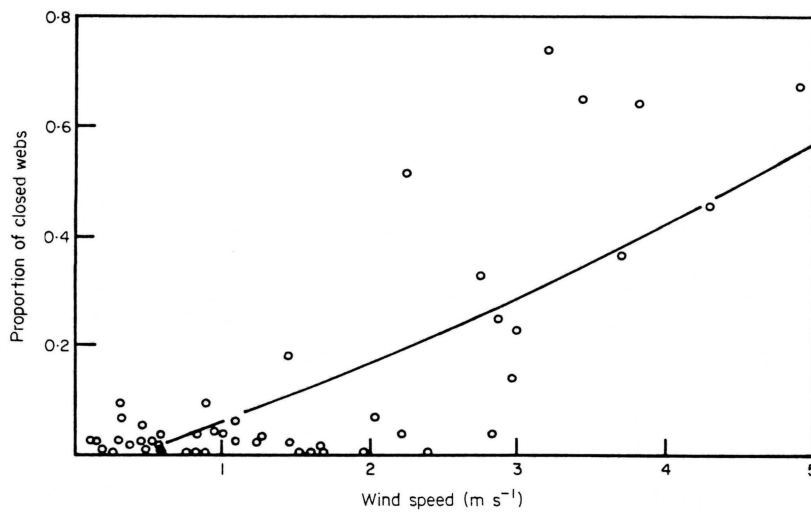


Figure 3. Relationship between the proportion of webs completely covered by sand (no capture lobes visible on the surface) and average wind speed measured over approximately 1 h during the census. $n = 54$ censuses on three dates of approximately 150 webs at Visnara.

daily maximum temperatures at 5 cm at Gobabeb were $51.2 \pm 5.3^\circ\text{C}$ in summer (December–April) and $38.5 \pm 5.4^\circ\text{C}$ in winter (May–November). During 1988 and 1989, we found that 91% of all juvenile dispersal at Visnara ($n = 2008$ new webs) occurred during September–November, when the upper layer of sand was relatively cool. Burrow depth varied with season: in winter, burrows were shorter than in summer (11.6 ± 0.1 vs. 13.2 ± 0.1 cm, $t = 8.59$, $df = 606$, $p < 0.001$). The change in burrow depth was especially evident with dispersing young. As maximum daily sand temperatures increased from September to November (41.2 ± 0.8 to $48.9 \pm 0.7^\circ\text{C}$ at 5 cm depth), dispersing juveniles built deeper burrows (7.8 ± 0.6 vs. 10.8 ± 1.1 cm, $t = 5.31$, $df = 154$, $p < 0.001$).

Influence of wind

The influence of wind on webs and spider activity was examined on daily and annual time-scales. We determined the wind speed at which webs became covered with sand and recorded the proportion of spiders with closed webs due to wind-blown sand in areas exposed to different wind regimes. By manipulating the levels of sand-loading on webs in these areas we examined the effects of changes in surface level of the sand on web-renewal behaviour.

During a gradually increasing wind at Visnara, a 1.0 ± 0.3 m s⁻¹ wind near the ground covered the first lobes of 16 webs that we monitored. A wind of 1.8 ± 0.3 m s⁻¹ covered 50% of the webs completely and repeated gusts at $1\text{--}2$ m s⁻¹ soon covered all webs with sand. These wind speeds are equivalent to $2.8\text{--}5.5$ m s⁻¹ measured at 1 m height above the ground.

The proportion of webs ($n = 150$) that were covered at different times of day was correlated with local wind speed ($r^2 = 0.60$, $p < 0.001$; Fig. 3). The effect of wind varied with time of day, following the pattern of increased wind speeds in mid-afternoon (Lubin & Henschel, 1991), and with location and census date. One area was consistently exposed to afternoon winds and, over the entire study period, 35% of the webs were covered compared to 11% in the sheltered area ($\chi^2 = 19.5$, $p < 0.01$). On sampling days 1 and 3, when afternoon winds reached 4.3 and 4.9 m s⁻¹ respectively, 27–30% of the webs were

covered in the afternoon, while at other times of day only 2–3% were covered. On day 2, there was little wind (maximum 2.0 m s^{-1}) and only 1–3% of the webs were covered in the afternoon.

Sand-loading

We tested the effect of sand-loading of *S. henscheli* webs in three areas at Visnara. Sand accumulated with time on both the experimental and control webs (Fig. 4), but the accumulation was greater on the former (ANOVA, $F = 106.6$, $p < 0.001$). The degree to which sand accumulated on webs differed also between areas (Fig. 4): in a wind-sheltered area, significantly more sand accumulated on experimental webs than in two wind-exposed areas (ANOVA, $F = 28.5$, $p < 0.001$) where the sand was regularly removed by afternoon winds.

Most web size parameters decreased with increased sand-loading except the widths of capture lobes, which were unaffected. The number of open lobes decreased with time in the experimental group, but remained constant in the control group. Overall, sand-loaded webs had fewer lobes (1.97 ± 0.08) than control webs (3.30 ± 0.06 , Kruskal-Wallis, $H = 138.7$, $p < 0.001$) and their surface mats were significantly shorter at the end of the experiment (sand-loaded $30.3 \pm 2.0 \text{ mm}$, control $41.2 \pm 2.5 \text{ mm}$; $H = 8.8$, $p < 0.003$). Spiders in the sand-loaded group often constructed upward extensions of the lobes to reach the new surface level ($n = 21$ spiders).

Wind scouring may present more serious problems to spiders than the heaping up of sand on the webs. Where spiders from sand-loaded webs in the two wind-exposed areas extended their mats up to reach the new surface, scouring by afternoon winds often

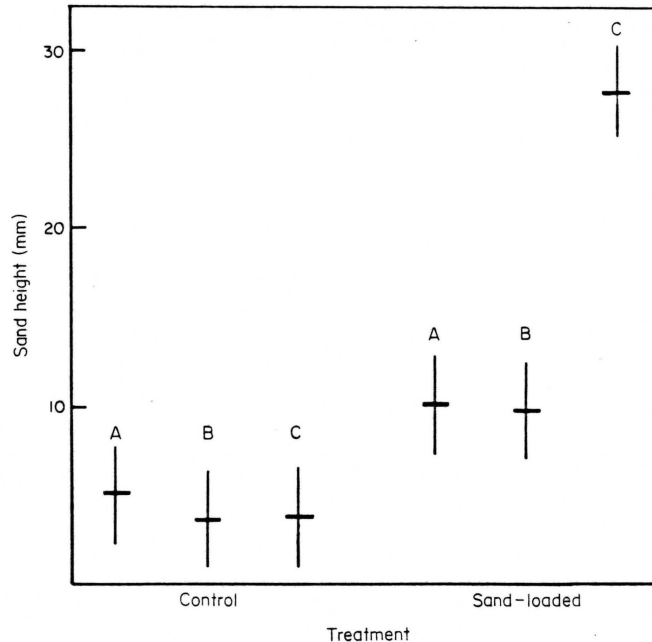


Figure 4. Change in sand height (mm) above control webs and sand-loaded webs at the end of the 14 day sand-loading experiment. Means and 95% C.I. are shown for webs in three areas of differing wind exposure at Visnara: areas A and B are exposed to wind, area C is wind-sheltered. $n = 10$ webs in each group.

Table 3. Web size variables ($\bar{x} \pm S.E.$) from two wind-exposed dune sites (Khommbabes and Visnara) and from a sheltered site in the Kuiseb River during the course of a year. Due to the bimodal size distribution of spiders, results are shown separately for spiders with body lengths of ≥ 3 mm and < 3 mm. Differences were tested by ANOVA. Different letters following the means indicate that population means differ from one another

Variable	Khommbabes mean \pm S.E.	Visnara mean \pm S.E.	River bed mean \pm S.E.	ANOVA	
				F	p
(a) BL ≥ 3 mm					
Body length	6.5 \pm 0.1 a	6.4 \pm 0.2 a	6.6 \pm 0.2 a	0.4	NS
Mat length	43.4 \pm 1.2 a	40.6 \pm 2.0 a	57.7 \pm 2.0 b	27.0	<0.001
No. open lobes	2.6 \pm 0.1 a	3.1 \pm 0.1 b	3.7 \pm 0.1 c	54.9	<0.001
Capture silk	38.7 \pm 0.9 a	46.6 \pm 2.0 b	56.4 \pm 1.8 c	48.7	<0.001
n	312	100	150		
(b) BL < 3 mm					
Body length	2.3 \pm 0.02 a	2.4 \pm 0.03 b	2.5 \pm 0.04 b	4.0	0.02
Mat length	13.0 \pm 0.3 a	11.9 \pm 0.4 b	17.8 \pm 1.0 c	26.1	<0.001
No. open lobes	2.9 \pm 0.1 a	2.2 \pm 0.1 b	4.2 \pm 0.2 c	61.3	<0.001
Capture silk	14.8 \pm 0.4 a	14.8 \pm 0.8 a	26.0 \pm 1.8 b	41.1	<0.001
n	106	73	25		

exposed and undercut the chamber, causing it to collapse (32.5% of 40 webs on one date). In these areas, three of the experimental spiders moved to new web sites.

We examined whether the degree of exposure to wind affects webs in the long term. We compared webs ($n = 766$ webs) in bimonthly samples for a year at two wind-exposed dune sites at Khommbabes (K) and Visnara (V) and at a relatively sheltered site in the Kuiseb River (R). All web variables differed markedly between the sheltered and the exposed sites (Table 3). Wind-exposed webs had smaller surface mats and fewer lobes of smaller width.

As the length of the mat is correlated with spider size (see above), we compared the slopes of the regressions of surface mat length on body length for the three study sites, by testing for the homogeneity of the regression coefficients. The slopes did not differ between the K and V sites ($t = 1.93$, $p > 0.05$). However, the regression slopes of both exposed sites were significantly higher ($p < 0.001$) than that of the sheltered river site (V vs. R $t = 28.15$, $df = 362$; K vs. R $t = 36.82$, $df = 617$). Surface mats of spiders from the same size classes were on average 27% shorter at exposed sites; the differences were significant in five of 10 size classes (paired t tests, $p < 0.05$).

Seasonal activity and sand movement

Population density and activity of *S. henscheli* is seasonal [Fig. 5(a), (b)]. During 1988 and 1989 at Visnara, spiders dispersed during late winter (September–November) and foraged through summer (November–April) until many died or became inactive during winter (May–August).

We investigated two parameters of sand-moving winds in relation to this seasonal activity of spiders: the time of day and the magnitude of sand movements. During 1988 and 1989 at Gobabeb, strong, sand-moving winds (> 16 km h^{-1} at 2.5 m above ground) occurred between midnight and noon mainly during April–July ($> 40\%$ probability per day), with a maximum of 21 days in May 1988 [Fig. 5(c)]. This contrasts with 10–40% probability of strong night-time winds at other times of the year. As web repair is a

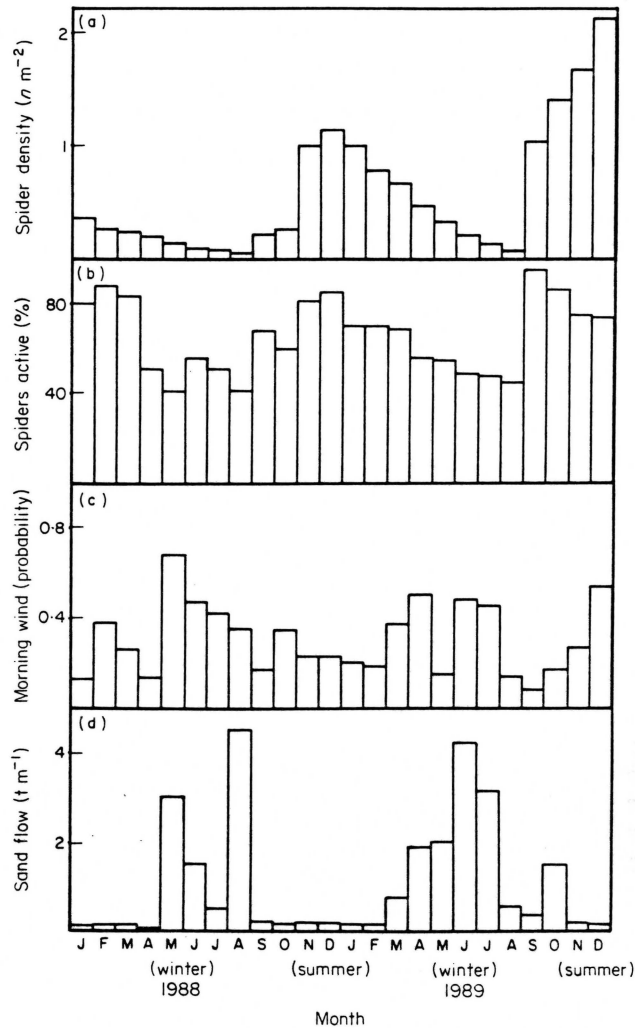


Figure 5. Seasonal changes during 1988 and 1989 at Visnara of (a) average spider density, (b) average proportion of spiders that were active on a calm morning, (c) average daily probability of a sand-moving wind occurring during the morning, 00.00–12.00 h, (d) total potential sand flow. Webs were monitored weekly, and continuous wind records were averaged per hour.

nocturnal activity, it is most likely to be disrupted during periods of strong post-midnight winds (early winter). This would prevent spiders from foraging the next day.

Changes in the sand surface level on shallow slopes are related to the potential rates of sand movement by wind (Bagnold, 1941; Lancaster, 1985). The degree of sand-loading or scouring of *S. henscheri* surface mats in wind-exposed areas can be predicted from the wind speed. For each month of 1988 and 1989, we summed the hourly values of potential sand flow from wind records obtained at Gobabeb [Fig. 5(d)]. Sand-moving winds occurred for 18% of the time (1542 h year⁻¹). During most winter months, the potential sand flow exceeded 1 t m⁻¹ month⁻¹, compared to less than 0.2 t m⁻¹ month⁻¹ in summer. One hour of strong winter wind (averaging 35–54 km h⁻¹) could cause 1–3% of the calculated annual potential sand flow; in 4 winter months this amounted to 75% of the annual flow [Fig. 5(d)].

These conditions also affected spider distribution. On the flat dune at Visnara, winter

winds caused sand surface levels to change up or down by up to 11 cm. However, we only found high densities of *S. henscheli* (five to 50 webs per 1 m² grid square; $n = 165$ squares) in stable areas where the surface had changed little (-0.6 to $+1.9$ cm, $\bar{x} = +0.5 \pm 0.02$ cm). The 44% of the squares where the level had changed by more than that (-2.7 ± 0.2 cm down or 3.1 ± 0.3 cm up) contained only 17% of the spiders ($n=390$, $\chi^2 = 29.6$, $df. = 1$, $p < 0.001$). For three successive winters (1988–90), these local patterns of change in surface levels at Visnara appeared to be similar. Unstable areas with few spiders were often in close proximity to stable areas with higher spider densities (0.9 ± 0.1 vs. 3.5 ± 0.7 spiders m⁻² respectively; $t = 3.39$, $df = 163$, $p < 0.001$). Most *S. henscheli* may avoid nearby potentially unsuitable areas by settling close to their maternal web.

Discussion

Not all organisms that live in the desert are uniquely adapted to it (Bradshaw, 1988). Traits that allow a web-building spider to inhabit shifting dune sand may be unique adaptations or they may be 'exaptations' (*sensu* Gould & Vrba, 1982) which occur more widely and, fortuitously, increase fitness of the desert species. The web of *S. henscheli* conforms, in its general structure, to the eresid pattern of a sheet with cribellar capture threads and a silk-lined, tubular retreat (Shear, 1986*b*). It deviates from the pattern seen in other ground-living eresids, e.g. *Eresus niger* (Norgaard, 1941), in that the capture threads of *S. henscheli* are not attached to the substratum. This modification is undoubtedly related to living in mobile sand which lacks fixed attachment sites. Although grass clumps are available in the habitats in which these spiders occur, *S. henscheli* does not anchor capture threads to vegetation. This may be due to the disproportionate scouring or deposition of sand by wind around large anchored objects.

For *S. henscheli* the main costs of building a new web are the material and labour (above resting metabolism) of constructing a new burrow and surface mat and the risk of dying while exposed on the surface or while digging a new burrow. Silk production is considered energetically expensive; it involves protein metabolism and the energetic cost of activity (Lubin, 1973, 1986; Prestwich, 1977). We suggest that most of the 6.5% loss of body mass per new web in *S. henscheli* was related to web construction. Spiders generally have a low resting metabolic rate (Greenstone & Bennett, 1980) and can tolerate long periods without food (Anderson, 1974). Two *S. henscheli* that were kept in vials without sand and inadvertently food-deprived, survived for 3 months and established new webs when finally released onto sand. In view of this, the mortalities in 3–4 weeks of some experimental spiders that repeatedly built new webs suggests a significant depletion of energy reserves.

Risk of predation on the surface is difficult to assess directly. It may be substantial, judging from the speed with which spiders released on the surface sought cover beneath a mat of woven silk and sand (<3 min after release). The time spent searching for a web site on the surface was significantly shorter after dark than at dusk at all sites. Alternative explanations for this difference are: (1) nocturnal predators are more abundant than diurnal ones. Crawford & Seely (1987) found approximately equal numbers of diurnal and nocturnal carnivorous arthropod species in the Namib dunes; however, they did not record numbers of individuals. Large, nocturnal spiders and scorpions may be more abundant than similar diurnal species (Henschel, 1990*a*). The fact that male *S. henscheli* search for mates on the surface during the day, rather than at night, also suggests greater predation risk at night. (2) Only limited time is available for burrowing sufficiently deep to escape heat stress in summer (Lubin & Henschel, 1991). Darkness may be a cue to begin construction immediately, as is the case in some other web-building species (Cloudsley-Thompson, 1987).

For most web spiders, web dimensions change with spider size and age (Witt *et al.*, 1968, 1972; Eberhard, 1990; Lubin *et al.*, 1991). Both habitat structure and prey type have

been shown to influence web geometry in some orb-weaving species, but the evidence (particularly for the latter factor) remains controversial (Eberhard, 1990). Webs of *S. henscheli* have much simpler geometries than those of orb-weavers; therefore, this species may be ideal for testing the effects of different environmental factors on web geometry.

In *S. henscheli*, spider size explained much of the variation in certain morphometric traits of the web, but not in others. The average capture lobe width correlated strongly with spider length (body length = $1.16 + 0.44 \times$ lobe width; Table 1). This is, therefore, a useful indicator of spider size in field studies where disturbance of the spider is undesirable. The size of the surface mat was related to spider size, but also depended on the duration of residence in the web and wind-related stresses.

Burrow length and the number of capture lobes correlated only poorly with spider size. Burrow length is a function of the thermal gradient in the sand and the cost of burrowing and web construction. Spiders that were released at dusk always dug burrows that were deeper than the minimum required for thermoregulation and only failed to do so when forced to dig several new burrows in short succession. The number of exposed capture lobes varied with habitat (Table 3) and with food availability (Lubin & Henschel, unpubl.). Variation among habitats may be due to different prey types prevalent in them, or to differences in overall prey availability. The geometry of the capture lobes, i.e. their spatial arrangement as well as their number, appears to differ among habitats (pers. obs.), possibly in response to directional prey movement.

High surface temperatures restrict foraging activity in *S. henscheli*: spiders are less prone to attack prey at surface temperatures $>65^{\circ}\text{C}$ (Lubin & Henschel, 1991). Nonetheless, shuttling between the cool burrow and hot surface allows the spider to continue foraging at very high temperatures. The apparent preference of *S. henscheli* for shadier web site locations may be due to either direct influences of surface temperature on foraging or to the distribution of prey. Further experiments are necessary to distinguish between these possibilities.

Dispersal and web site relocation may also be influenced by temperature at the surface. Males search for mates in daytime only during the cooler months, when maximum sand-surface temperatures averaged 44.2°C (in May; Seely & Stuart, 1976). Dispersal of juveniles from the parent burrow also occurs in the cool season, and burrow depth increases with increasing surface temperatures. As burrow depth is not scaled to body size, the cost of burrowing for a dispersing juvenile is greater than for an adult, and there may be strong selection on dispersal to coincide with the cool season.

Wind direction and strength has been shown to influence the placement of orb webs in some species (Eberhard, 1971, 1990). It is also suggested as a selective factor in determining orb-web geometry (Langer, 1969; Craig, 1989). Experimental evidence is generally lacking, partly because of the difficulties of manipulating wind or wind-related damage independently of other factors. For webs of *S. henscheli*, the consequences of strong winds are either sand-loading or scouring. Spiders may adapt to periodic, heavy sand-loading events by extending their capture lobes up to the new surface. This happens more frequently at sites that are exposed to strong winds than in sheltered locations. Our manipulations of sand-loaded webs suggest that repeated extension or renewal of the mat entails an energetic cost. This is reflected in a reduction in the size of most surface mat variables. Thus, shorter surface mats with fewer capture lobes characterised webs in the exposed dune areas of Visnara and Khommabes relative to those in the wind-sheltered habitat of the Kuiseb River bed. Webs were rare or absent on upper dune slopes where sand movement is greatest (Lancaster, 1985).

The minimum wind speed that covered *S. henscheli* webs agrees with the threshold wind speed for sand movement determined in previous studies (Lancaster, 1989). On a daily basis, we showed that sand-loading limits foraging activity in the late afternoon when sand-surface temperatures are moderate and foraging would otherwise continue. However, this is probably not a critical loss of foraging opportunity, as the activity of the major prey, ants, also decreases or ceases altogether under the same conditions (Curtis, 1985a,b;

Marsh, 1985, 1988) and the capture silk can be renewed at night. In contrast, winds that occur at night or in the morning may disrupt foraging for the entire day.

Seasonally strong wind such as the dry, east winds in winter (Lancaster *et al.*, 1984; Lancaster, 1989) disrupt *S. henscheli* activity by sand-loading or scouring webs for extended periods of time. This season coincides with egg-laying and tending of young in sealed brood chambers (pers. obs.). However, this is not unique to this species, as other eresids typically reduce their foraging activity during the egg-laying season (e.g. *Stegodyphus lineatus*, (pers. obs.); *Eresus niger*, Norgaard, 1941). Nonetheless, juvenile dispersal begins only after these disruptive winds have ended, suggesting a causal relationship between the annual wind regime and seasonal activity in *S. henscheli*.

In summary, the web of *S. henscheli* provides the necessary conditions for foraging at most times of day when prey species are active on the sand surface. However, web design and spider activity are influenced by local and seasonal wind conditions, mainly due to the effects of sand deposition and scouring. Webs of *S. henscheli* are patchily distributed in space, reflecting, in part, the effects of abiotic factors. Local clustering may be the result of active site selection during dispersal, or simply an outcome of increased survival and reproduction at favourable sites coupled with restricted dispersal (Partridge, 1978). We have shown that web relocation for *S. henscheli* is costly, both energetically and in the potential risk of predation. Frequent web relocations are not expected to occur under such conditions (Janetos, 1986). This suggests that the observed distribution of webs is the result of reduced dispersal and differential survival rather than active web site selection. Further studies are in progress to examine these alternative hypotheses.

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