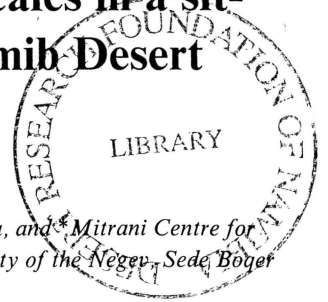


# A test of habitat selection at two spatial scales in a sit-and-wait predator: a web spider in the Namib Desert dunes

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## Summary

1. Distribution and web characteristics were examined for the dune-burrowing spider *Seothyra henscheli* in the Namib Desert to determine how these spiders relate to spatially heterogeneous habitat features that influence foraging costs and benefits, growth rate and survival. In particular, we set out to determine the relative importance of (i) habitat selection, (ii) site-dependent growth and survival, and (iii) restricted dispersal, to the occurrence of *S. henscheli* in different macro- and microhabitats.
2. Spider webs were mapped along transects that crossed dune regions with dense vegetation hummocks, steep dune plinths and bare, gravelly interdune plains. Spiders were more abundant in the hummocks than in the interdunes and plinths. Translocation of spiders from the hummocks to the interdunes and plinths confirmed that spider density was correlated with habitat quality.
3. In a comparison of web sites with dummy sites in terms of factors related to sand stability and food availability, it was found that, except for the avoidance of extreme conditions, web-site characteristics did not differ from dummy sites. Web geometry indicated that good sites were characterized by stable sand and abundant ants. However, many spiders occurred at poor sites when good sites were vacant nearby.
4. It is concluded that *S. henscheli* do not actively choose web sites, but have restricted dispersal. Site-dependent growth and survival may explain the pattern of local abundance. Site tenacity may be a result of the spiders' inability to predict site quality coupled with high costs of relocation. It is inferred that spiderlings tend to remain near their mother's site, which has a previous record of success.
5. Tolerance of variable conditions of dunes and the ability to sustain populations even at poor sites enable these spiders to occur in extreme desert conditions.

*Key-words:* Eresidae, habitat quality, *Seothyra henscheli*, site-dependency, spatial scale.

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## Introduction

A non-random spatial distribution of organisms can provide information about their relative success in different habitats and suggest which features of the habitat contribute to their success. Resources (food, nesting sites) on the one hand and refuge from enemies and from climatic extremes on the other, should ultimately determine the pattern of distribution (Pulliam 1989). Empirical and theoretical studies address the mechanisms and adaptive consequences of active habitat choice in a wide variety of organisms. It is often assumed that animals sample habitat patches

during the dispersal phase and then choose among available patches based on cues that indicate habitat quality (Partridge 1978).

One way to describe habitat selection is to compare variation in specific habitat features at particular spatial or temporal scales with the distribution of individuals of the target species (e.g. Orians & Wittenberger 1991). A significant relationship between distribution and habitat variables may indicate that the particular variables measured are relevant to active habitat choice of dispersers at that scale. Alternative hypotheses that yield similar relationships are that the observed distribution is the result of differ-

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ential mortality and reproduction or that it is a consequence of historical factors such as a particular mode of dispersal.

Habitat selection in sit-and-wait predators such as some web-building spiders may determine lifetime fitness, because movements to new web sites occur only once or at most a few times in their lifetime (Riechert 1976; Tanaka 1989; Lubin, Kotzman & Ellner 1991; Lubin, Ellner & Kotzman 1993; Ward & Lubin 1993). There are two general solutions to the problem of site selection for web spiders: first, site selection may be quite precise, leading to strong correlations between distribution and habitat features that determine fitness; and secondly, spiders may tolerate a wide array of conditions, adjusting their behaviour and physiology accordingly (Vollrath 1985, 1986). In the latter case, site selection may not be as precise, but the spider's condition will vary with habitat quality.

We examined the possibility of habitat selection in a dune-burrowing spider, *Seothyra henscheli* Dippenaar 1990 (Eresidae). *Seothyra* maintains a sticky capture web in shifting dunes. The sand-dune habitat is relatively simple physically and offers an opportunity to assess correlations between habitat features, spider distribution and fitness. For *S. henscheli* the relevant features of the habitat are temperature, wind and food. High sand-surface temperatures limit foraging activity of *S. henscheli* and wind-blown sand regularly covers the webs, which must be repaired daily (Lubin & Henschel 1990; Henschel & Lubin 1992). The Namib Desert dunes are characterized by low insect biomass (Louw & Seely 1982; Seely 1991) and encounters with prey may be infrequent (Lubin & Henschel 1996). Web relocation occurs only infrequently and is costly in terms of silk production for a new burrow and web, and there is a risk of being captured by predators during movement on the surface (Henschel & Lubin 1992). Thus, we anticipated that *S. henscheli* will select habitats using cues that reflect habitat quality *vis-à-vis* temperature, wind and prey abundance.

Sand flow (the amount of sand shifted by wind), prey and predators appear to vary on a relatively small spatial scale in the Namib dunes (Lancaster 1989; Seely 1991). At the immediate site of a web, topographical structures may modify wind speed or direction and influence sand flow. Compactness of the substrate, slope and vegetation may affect the thermal environment as well as sand flow. The abundance of prey and predators and density-dependent factors, such as intraspecific competition, may also interact with these physical features. Does *Seothyra* recognize spatial variation in some or all of these characteristics, and can it select web sites based on cues that indicate habitat quality?

We considered the distribution of *S. henscheli* at two different spatial scales. The larger scale was based on major physical and biotic discontinuities in the

spider abundance over distances of tens of metres; the smaller scale was that of the spider's web site and its immediate surroundings. We addressed the following questions. How does the abundance of *Seothyra* vary in the different dune habitats? What constitutes a suitable web site? Do web sites and web characteristics differ among habitat types? We investigated these questions by: (i) mapping the occurrence of spiders across dune landscapes; (ii) characterizing habitat conditions that relate to food, near-surface winds and sand flow at web sites and at sites selected randomly; (iii) relating web parameters to these features; and (iv) comparing the foraging activity, growth and survival of spiders that were shifted between different habitats. The latter experiment was designed to test whether spatial differences in spider density are a consequence of differences in site quality. Possible density-dependent effects (e.g. interference competition) on the distribution of spiders are the subject of a separate study.

## Methods

### SEOTHYRA NATURAL HISTORY

*Seothyra henscheli* is restricted to sandy substrates of the Namib Great Sand Sea (Dippenaar 1990). The spider constructs a silk-lined burrow in sand (see descriptions in Lubin & Henschel 1990; Henschel & Lubin 1992). The burrow entrance is concealed beneath a dense silk mat that is continuous with the burrow lining and may be considered an extension of the burrow entrance (Peters 1992). The silk mat on the surface is elongated and has one or more rounded lobes at each end. These lobes are lined with sticky, cribrate silk and form the capture web, designated 'capture lobes' (Fig. 1). The resemblance of this arrangement to a mammal footprint is the basis of the spider's colloquial name of spoor spider. Prey walking or landing on the sand surface becomes trapped in the sticky capture lobes and is seized by the spider from beneath the capture mat, pulled beneath the mat and from there into the burrow.

*Seothyra henscheli* is annual or biennial (Henschel & Lubin 1992; Lubin & Henschel 1996). Females mature and reproduce during early winter (May–June) at a body length of 7–13 mm and a mass of 58–239 mg ( $n = 56$  individuals). The number offspring ranges from 19 to 29 ( $n = 3$  clutches). The offspring overwinter in the maternal burrow; initially they are fed by the mother, and eventually they consume her. The juveniles disperse from the maternal burrow in early summer (October–November).

### SURVEY AT KHOMMABES

The main study was conducted at Khommabes, 6 km west of Gobabeb, in the Namib Great Sand Sea. We surveyed webs across a dune landscape encompassing a range of habitats (Robinson & Seely 1980; Teller



Fig. 1. Web of *S. henscheli* with four capture lobes on the sand surface. The scale is in cm.

& Lancaster 1985; Seely 1991) in which population densities of *S. henscheli* varied naturally. We censused three transect lines (each 1500 m long) that extended from halfway down the plinth of a large longitudinal dune eastwards across a valley to the next dune plinth (Fig. 2). Each line was divided into contiguous, 30-m long segments, which were regarded as the sample units for most analyses. The five major habitats and vegetation cover estimates (J.R. Henschel and M.K. Seely, unpublished data) were as follows.

#### Dune plinth

Steep (10–20°) flanks of linear dunes on the western and eastern edges of the study area, sparsely vegetated

(2% cover) with the tall grass *Stipagrostis sabulicola* (Pilger) De Winter.

#### Dune base

Gently sloping (<10°) lower parts of linear dunes, vegetated (3% cover) with shorter grasses *Stipagrostis gonatostachys* (Pilger) De Winter, *Stipagrostis lutescens* (Nees) De Winter, *Stipagrostis sabulicola* and *Cladographis spinosa* Phillips, and the occasional leaf succulent *Trianthema hereroensis* Schinz.

#### Interdune plain

Relatively bare, gravel-strewn sandy valley between dunes with scattered dwarf shrubs *Salsola* sp. (<1% vegetation cover).

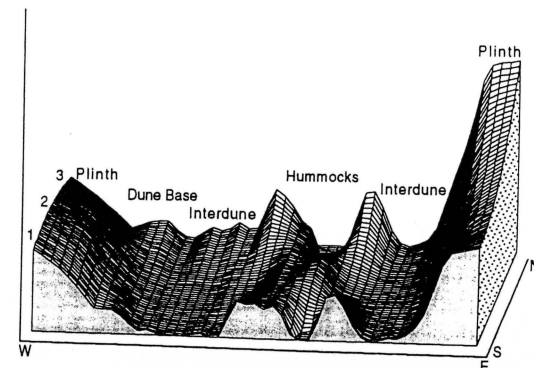


Fig. 2. Southerly view of a three-dimensional surface map of the Khommabes study area (height and slope exaggerated, height of western plinth c. 30 m). The relative positions of various dune habitats along three 1500-m long transects (numbered) are indicated.

### Exposed hummocks

Accumulations of sand around 5–10-m high Nara plants *Acanthosicyos horridus* Welwitsch-ex Hook (Cucurbitaceae) that are moderately vegetated (11% cover) with *Stipagrostis sabulicola* and *T. hereroensis*. This region is exposed to north-east storm winds.

### Dense hummocks

Nara hummocks with dense tussocks of *Stipagrostis sabulicola* and *T. hereroensis* (21% cover) situated east of the exposed hummocks. This region is relatively protected from north-east winds.

The census method was as follows. Two observers walked along a transect line from west to east 0–3 h after sunrise (the webs are best seen in the oblique morning light). Each *S. henscheli* web found within 2 m of the centre of the transect line was marked and numbered. Webs seen outside the 2-m limit during this initial walk were recorded, but not marked, as were webs within the transect area that were found after the initial census walk. These additional webs were used to determine the presence of *S. henscheli* in areas where webs were not seen on the census and served also to check the accuracy of the census.

Web and web-site characteristics were recorded at a sample of web sites (web measurements follow Henschel & Lubin 1992). Web variables were: length of the surface mat, width of the capture lobes, and orientation of the long axis of the surface mat; web-site variables were: habitat type, slope direction and inclination, compaction of the substratum, elevation of the near horizon due to topography in four cardinal directions, presence within 2 m of vegetation in three size classes, whether webs were on vegetation hummocks, and sand flow (see below). Where there were fewer than five webs per 30-m segment, all webs were measured; where there were more, a random sample of five webs was measured. Altogether 295 webs out of a total of 659 were measured. A similar set of habitat measurements was obtained from a dummy site located 4 m from the start of each segment ( $n = 150$  segments along three lines). The measured web located nearest to each dummy site (mean  $\pm$  SD distance 5.3  $\pm$  5.5 m, range 0–22 m) was chosen for comparison.

Three measures were devised to assess relative exposure to winds that cause sand to shift. Shelter from wind due to topography was assessed as elevation of the near horizon, using a gridded double-mirror system. Two mirrors (each 120 mm  $\times$  80 mm) were fixed lengthwise at a 100° angle to each other and kept horizontal with spirit levels. When placed flat onto the ground, each mirror projected 40° from the surface plane. Looking onto this from straight above the joint of the mirrors, an observer counted the number of grids on each mirror that were covered by reflections of nearby landscape objects (<30 m

distant) projecting above the level of the site to be assessed. The higher and closer an object was, the more grid squares its reflection covered on the mirror. The 30-m cut-off distance was chosen arbitrarily as the stretch in which wind speeds are reduced by >50% in the lee of 10-m high hummocks (Oke 1978; Lancaster 1989).

A second method was to measure sand flow using sand traps: 15-mm diameter vials were inserted vertically into the sand with the open rim level with the surface. The volume (ml) of sand accumulated in a day was proportional to the amount of sand moved by wind at the site. Three measures were obtained at each site.

A third method was to measure the change in sand surface height over the season of north-easterly storm winds between May and October (Lancaster 1989; Henschel & Lubin 1992). The above-surface heights (cm) of the poles that demarcated each segment along the study lines were measured in March and again in October. The difference in pole height was due to sand deposition or deflation (wind-eroded troughs) during the intervening stormy period. To compare these patterns with the distribution of spiders, it was assumed that the general patterns of sand surface change, determined after the current spider census, were similar to the previous patterns to which the spider population had responded (Henschel & Lubin 1992). This is a reasonable assumption in view of the fact that north-east storms are a regular annual phenomenon (Lancaster 1989).

Compaction of the substratum was determined with a spring pressure gauge fitted with a round tip consisting of half a table-tennis ball (36 cm diameter) filled with rubber. The hemispherical tip was pushed into the sand until it was immersed level with the surface and a pressure reading ( $\pm 0.075$  kPa) was taken. Measurements ranged from 0.225 kPa for unconsolidated sand of a dune slipface, to 4.125 kPa for interdune gravel.

Potential prey abundance was estimated by direct census. At Khommabes, the ants *Camponotus detritus* Emery (live mass 24.4  $\pm$  1.7 mg; Lubin & Henschel 1996) and *Tetramorium rufescens* Stitz (1.7  $\pm$  0.1 mg,  $n = 18$ ) are the most important prey. As these ants both have peaks of activity during early to middle morning (Curtis 1985a; Marsh 1988; personal observation), surface-active ants were counted between 08.00 and 10.00 hours along the same transect lines (and widths) as for the spider census. The censuses were repeated on three mornings along each line.

### SURVEY AT HARUBES

For comparison with the Khommabes data, a survey was conducted on the north-facing lower slope of a star dune (>100-m high dune with multidirectional ridges) at Harubes, 45 km southeast of Khommabes. In this region, *S. henscheli* webs were abundant, but

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the wind patterns, vegetation and faunal assemblage patterns differed from Khommabes (Seely, Ward & Marais 1989; present study). The same techniques were used as at Khommabes, except for assessing ant abundance, which was done using pit-traps (buckets of 15 cm diameter) which were checked after one day. The two transect lines at Harubes were each 210 m long.

### SPIDER TRANSLOCATIONS

To test whether spider density in a habitat reflected the quality of the habitat, spiders were relocated from the hummock region at Khommabes to three habitats: interdune ( $n = 25$ ), plinth ( $n = 24$ ) and hummock ( $n = 21$ ). The latter group served as a control for the interdune and plinth groups. The translocated spiders as well as a sample of spiders found naturally in the habitat were monitored over a period of 6 weeks following the translocation.

Body length and mass of captured spiders were measured. While releasing them, we recorded the time and distance from release until each spider began constructing a burrow. The number of capture lobes and excavated burrows to retrieve the spiders and measure spider length and body mass. If burrows were unoccupied, we attempted to determine the cause: a destroyed web, or signs of predators at or in the web could indicate predation, the presence of a dead spider indicated other causes (e.g. starvation or overheating).

### DATA ANALYSIS

Each 30-m segment was treated as a sample unit. The independence of samples was tested by autocorrelation of environmental variables lagged 1 and 2

segments. Adjacent segments and segments once removed were correlated ( $r = 0.28$  and  $r = 0.31$ , respectively,  $P < 0.001$ ). This was probably because they were usually situated in the same macrohabitat.

Many variables were not normally distributed and were transformed (Table 1). When transformation still did not yield normality, Kruskal–Wallis one-way analysis of variance (test statistic indicated by H) and Wilcoxon Mann–Whitney two-sample test ( $z$ -value, 2-tailed) were used (Siegel & Castellan 1988). Principal components analysis (PCA; Dunteman 1989) was applied to the environmental data measured at web sites to determine those factors that were associated most strongly with the sites. Missing values were not substituted (Table 1).

Three web parameters were selected as indications of the spiders' responses to environmental conditions at different time scales (Henschel & Lubin 1992; Lubin & Henschel 1996). These were the number of capture lobes, which may change from day to day; web length, changing during the period of a week; and capture lobe width, which may change in the course of several weeks (Henschel & Lubin 1992; Lubin & Henschel 1996). Of these variables, lobe width was the most highly correlated with body size. To remove the effect of spider size on web length, the residuals of the regression of web length on capture lobe width ( $r^2 = 0.64$ ,  $P < 0.001$ ) were used. Means are given  $\pm 1$  SD and medians  $\pm$  one quartile.

### Results

#### KHOMMABES HABITAT DESCRIPTION AND SPIDER DISTRIBUTION

Measures of spider abundance and of habitat variables at Khommabes are summarized in Table 2. The average density of *Seothyra* was 0.073 m<sup>-2</sup> (range 0–

Table 1. Names and descriptions of variables measured. P/A = presence/absence

Variable	Description	Range	Transformation
Spider abundance	Number of <i>Seothyra</i> counted in segment	0–88	$\log_{10}(N + 1)$
Ant abundance	Number of ants counted in segment	0–300	$\log_{10}(N + 1)$
Slope	Surface inclination above horizontal	0–33°	arcsine
Aspect	Compass direction of slope >9° uphill	1–360°	sine
Compaction	Pressure required to penetrate sand	0.2–4.1 kPa	arcsine
Horizon elevation	Area on mirror of topography <30 m	0–100%	arcsine
Sand flow	Volume collected in sand traps	0–80 ml	arcsine
Deflation	Surface lower after windy season	1–30 cm	none
Deposition	Surface higher after windy season	1–26 cm	none
Small plant	<10 cm high plant within 2 m	0–1	P/A
Medium plant	10–100 cm high plant within 2 m	0–1	P/A
Large plant	>100 cm high plant within 2 m	0–1	P/A
Hummock	Site is on/off a vegetation hummock	0–1	P/A
Web length	Maximum length of surface mat of web	10–120 mm	residual
Entrances	Number of open lobes to a web	1–6	none
Entrance width	Median width of web entrance lobes	2–32 mm	$\log_{10}(X)$
Orientation	Compass direction of web long axis	1–180°	sine

**Table 2.** Abundance of *S. henscheli* and of two species of ants, *C. detritus* and *T. rufescens*, and measurements of environmental variables at dummy sites in five habitats at Khommabes: (a) number of segments and total abundance of spiders and ants, (b) medians (maxima) of variables, and (c) percentage of segments in which particular variables were present

	Plinth	Base	Interdune	Exposed humm.	Dense humm.	Overall
<b>(a) Total counts on census</b>						
Segments	15	26	44	27	38	150
<i>Seothyra</i>	4	17	81	72	485	659
<i>C. detritus</i>	190	381	174	760	1324	2829
<i>T. rufescens</i>	0	0	48	348	509	905
<b>(b) Median (maximum)</b>						
<i>Seothyra</i>	0 (3)	0 (4)	1 (8)	1 (13)	9 (88)	1 (88)
<i>C. detritus</i>	6 (46)	4 (98)	0 (83)	20 (92)	16 (204)	7 (204)
<i>T. rufescens</i>	0 (0)	0 (0)	0 (21)	0 (299)	1 (285)	0 (299)
Slope	12 (22)	5 (11)	3 (15)	8 (33)	9 (32)	5 (33)
Compaction	1.6 (3.2)	2.0 (3.3)	2.1 (4.1)	1.8 (2.7)	1.6 (4.0)	1.8 (4.1)
Horizon	20 (38)	3 (36)	0 (25)	44 (78)	56 (98)	14 (98)
Sand flow	29 (80)	20 (35)	2 (29)	29 (54)	7 (61)	14 (80)
Deflation	2 (5)	1 (7)	1 (2)	4 (30)	3 (17)	2 (30)
Deposition	3 (5)	2 (3)	2 (3)	6 (26)	2 (6)	2 (26)
<b>(c) Percentage presence</b>						
<i>Seothyra</i>	20	46	59	70	90	63
<i>C. detritus</i>	93	77	43	100	100	79
<i>T. rufescens</i>	0	0	20	26	53	24
Deflation	27	23	2	41	34	23
Deposition	27	15	7	33	29	21
On hummock	0	0	0	22	32	12
Small plant	20	58	0	30	18	22
Med. plant	20	31	0	48	37	25
Large plant	7	0	0	26	55	19
Slope >9°	87	4	4	37	50	30

1.5 m<sup>-2</sup> in 30-m long segments). The three major habitat types (hummock, interdune and plinth) differed significantly in the abundance of spiders and of ants ( $H > 32$ , d.f. = 4,  $P < 0.001$ ). Slope, horizon height and sand flow also differed significantly among the habitats ( $H > 49$ , d.f. = 4,  $P < 0.001$ ). Sand compaction and the degree of surface-level change with time (deflation or deposition) did not differ between habitats ( $P > 0.05$ ), but the variance of surface-level change was greater in the hummocks than in the other two habitats ( $F > 4.4$ ,  $P < 0.01$ ). Sand flow, measured near spider webs, differed between habitats ( $H = 12.28$ , d.f. = 2,  $P = 0.002$ ), with the interdune tending to have lower values than the plinth and hummock regions ( $z > 2.92$ ,  $P < 0.005$ ).

The single census revealed some 85% of the spider population: an additional 115 webs were found on the transect lines after the survey. Of 659 spiders counted on the census, most (84.5%) occurred in the hummock region (Table 2). Significantly more spiders were found in the hummocks than expected based on the area occupied by this habitat ( $\chi^2 = 117$ , d.f. = 1,  $P < 0.001$ ).

#### ENVIRONMENTAL CHARACTERISTICS AT WEB SITES

Web sites were located on gentle slopes (median = 5°, quartiles 3–9°). Only 13% of the webs were on mod-

erately steep slopes of 11–23°. There was no trend with respect to slope aspect ( $\chi^2 = 9.3$ ,  $n = 8$  classes,  $P = 0.31$ ,  $H_0$  = even distribution) and, consequently, slope aspect was excluded from further analyses. The sand at web sites was usually lightly compacted, yielding at  $1.46 \pm 0.64$  kPa. The horizon around webs was high ( $38.6 \pm 27.7\%$ ), particularly to the north and south where over 40% of the values exceeded 50%. Most (70%) web sites occurred near plants, with medium plants being most common (31%), followed by small (26%) and large plants (16%).

The abundance of spiders in each segment was significantly correlated with the abundance of the ants *Camponotus detritus* ( $r = 0.32$ ,  $P = 0.0001$ ) and *Tetramorium rufescens* ( $r = 0.26$ ,  $P = 0.001$ ). The total number of *S. henscheli* recorded in each habitat, however, was correlated only with the total number of *C. detritus* ( $r = 0.89$ ,  $P = 0.044$ ) and not with *T. rufescens* nor with all ants together ( $P > 0.05$ ).

PCA of the web-site variables yielded four uncorrelated components (axes) which together explained 65% of the variation in the data. The directional near-horizon elevations to the south, north and west, slope and the occurrence of large plants dominated the first axis, the occurrence of large, medium and small plants the second, eastward horizon the third, and sand compaction and slope the fourth axis (Table 3). A similar pattern was found in PCA of each of the sandy habi-

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**Table 3.** Score coefficients of the first axes of PCA of environmental variables for *Seothyra* webs at Khommabes and at Harubes. Bold indicates a strong association with that axis. Signs and magnitude of coefficients for each axis are relative and arbitrary

Study area	Khommabes				Harubes		
	1	2	3	4	1	2	3
Slope	-0.22	0.05	0.20	-0.50	-0.25	-0.21	-0.26
Compaction	0.16	0.13	0.08	-0.81	0.20	0.09	-0.28
Horizon N	-0.25	-0.05	0.28	0.07	-0.30	-0.08	0.02
Horizon E	-0.15	0.15	-0.80	-0.23	-0.18	0.33	0.19
Horizon S	-0.28	-0.04	-0.20	0.02	-0.13	0.16	0.38
Horizon W	-0.23	0.00	0.16	0.12	-0.21	0.20	-0.49
Small plant	-0.06	0.55	0.43	-0.01	0.07	-0.44	0.24
Med. plant	-0.09	0.60	-0.17	0.17	-0.25	-0.12	0.27
Large plant	-0.24	-0.33	0.09	-0.22	-0.12	0.45	-0.25
Variability (%)	30.8	13.6	10.6	10.5	29.8	17.2	14.8

tats separately (excluding the interdune), although there were differences in detail for the horizon and plant indices, as these differed between habitats. For the interdune, small plants and compaction were the dominant variables on the first three axes; horizon indices did not show a clear pattern.

#### WEB-SITE VARIABLES VS. SURROUNDING CONDITIONS

Measurements of environmental variables at a dummy site in each segment were compared with that of the closest *S. henscheli* web. There were no significant differences in the presence of small, medium or large vegetation near webs or dummy sites in the total sample and for each habitat separately ( $\chi^2 < 3.9$ , d.f. = 1,  $P > 0.05$ ). Where plants were present near sites, webs were no closer or further from plants than expected from a random distribution ( $t < 1.44$ , d.f. > 48,  $P > 0.05$ ). The means of horizon elevation and slope for each habitat did not differ significantly between web and dummy sites ( $t$ -test,  $P > 0.05$ ), but sand compaction and flow were lower at webs than dummy sites ( $t = 2.84$ ,  $P = 0.0044$  and  $t = 2.78$ ,  $P = 0.0055$ , respectively, d.f. = 241). The variances of slope and compaction differed significantly between web and dummy sites in the dense hummocks and, similarly, the variances of cover and sand flow on plinths (F-ratio,  $P < 0.05$ ). Webs were not found at sites with extreme values and web sites had lower variances than dummy sites for these characters.

The number of *S. henscheli* webs in a segment was correlated positively with horizon elevation, measured both at a web and at a dummy site ( $r^2 = 0.24$  and  $r^2 = 0.21$ , respectively,  $P < 0.001$ ). A negative relationship was found for sand flow (web site  $r^2 = 0.29$ , dummy site  $r^2 = 0.26$ ,  $P < 0.05$ ). There was no significant relationship with the degree of change in surface level over a 6-month period.

#### WEB GEOMETRY IN RELATION TO HABITAT

The orientation of the long axis of webs was not significantly different from random ( $\chi^2 = 3.4$ ,  $n = 8$  classes,  $P = 0.33$ ). The number of capture lobes per web, mean lobe width, and residual web length (after the effect of spider size was removed by regression of web length on lobe width) were compared for the three major habitat types: plinth (combined with dune base), interdune and hummock (exposed and dense combined). The number of capture lobes per web differed between habitats ( $H = 6.542$ , d.f. = 2,  $P = 0.038$ ) due to the difference between the interdune (median = 4) and the hummocks (median = 3,  $z = 2.55$ ,  $P = 0.0054$ ). Differences were not significant for lobe width ( $H = 0.713$ , d.f. = 2,  $P = 0.7$ ), nor for residual web length ( $H = 1.81$ , d.f. = 2,  $P = 0.4$ ).

No strong relationships were evident between web geometry and slope, compaction and horizon elevation ( $r^2 < 0.02$ ). Plots of residual web length and capture lobe width against sand flow (Fig. 3) showed an 'envelope' pattern (Goldberg & Scheiner 1993) and variances had a heteroscedastic distribution along the x-axis. This was analysed by comparing the points above and below the medians of the independent and dependent variables for each plot (Fig. 3). Neither residual web length nor the number of capture lobes differed significantly at high and low sand flow ( $\chi^2 < 1.84$ , d.f. = 1,  $P > 0.17$ ). However, the range of values of residual web length at high sand flow was only 42% of that at low sand flow (Fig. 3a). Lobe width differed significantly below and above median sand flow ( $\chi^2 = 4.20$ , d.f. = 1,  $P = 0.040$ ). Thus, there were significantly more wide-lobed webs at sites with low sand flow (Fig. 3b).

There were no significant relationships between web geometry (number of capture lobes, lobe width or residual web length) of a randomly selected web in a segment and ant abundance in that segment ( $r^2 < 0.046$ ,  $n = 78$ ,  $P > 0.05$ ). However, there was a

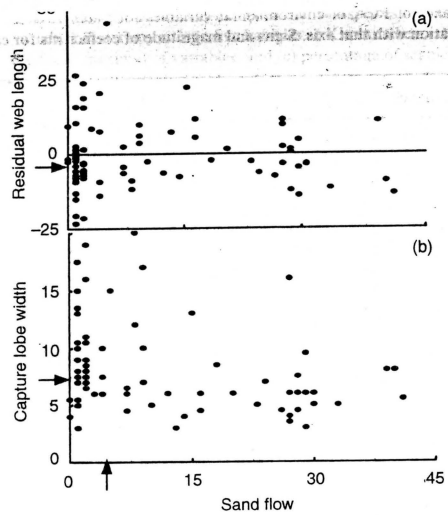


Fig. 3. Residual web length (a) and web entrance width (b) vs. sand flow measured at web sites of spiders. Arrows indicate the medians.

significant positive correlation between residual web length and ant abundance ( $r^2 = 0.16$ ,  $n = 44$ ,  $P = 0.006$ ) at sites where sand flow was low (< median). The web length of large spiders (capture lobe width > median) had a positive relationship with ant abundance ( $r^2 = 0.17$ ,  $n = 36$ ,  $P = 0.013$ ), whereas that of small spiders did not ( $P > 0.05$ ). Taking these effects together, the web length of large spiders (> median) at sites with little sand flow (< median) tended to increase with ant abundance ( $r^2 = 0.26$ ,  $n = 24$ ,  $P = 0.009$ ).

Web length and capture lobe width were measured

for resident spiders in the hummock, interdune and plinth regions ( $n = 22$ , 11, and 11, respectively) over 6 weeks (Table 4). Web length increased significantly more in the hummock and interdune habitats than in the plinth (Kruskal–Wallis,  $P < 0.05$ ). The differences were not significant for lobe width and residual web length.

#### NEAREST NEIGHBOURS

*Seothyra* webs had a significantly clustered distribution in all three main habitat types (standardized Morisita index of dispersion; Krebs 1989; plinth and dune base, 0.510; interdune, 0.508; hummock, 0.517). Fifty per cent of the 659 spiders counted on the transects had nearest neighbours within distances of <1 m, 76% within <2 m, and 95% within <9 m. There were, however, spiders whose nearest neighbours were up to 105 m away. Based on this distribution pattern of *Seothyra* webs, spider density was assigned to two classes: clustered (nearest neighbour  $\leq 2$  m) and remote (nearest neighbour > 2 m). Remote webs might be sole survivors of a previous cluster or they might be dispersers.

Remote webs were associated with positive scores of the PCA axis 1 (see above;  $\chi^2 = 12.34$ , d.f. = 1,  $P < 0.001$ ). This was because 80% of the remote webs were at sites with low horizon elevation (Fig. 4; cross-tabulation of  $\leq 50\%$  vs.  $> 50\%$  horizon cover:  $\chi^2 = 24.0$ , d.f. = 1,  $P < 0.001$ ) and at sites away from large plants. Only 49% of the remote webs were found in the hummocks, where 80% of the clustered webs occurred ( $\chi^2 = 31.8$ , d.f. = 1,  $P < 0.001$ ). Even within this habitat, remote webs were most frequently found at sites with low horizon ( $\chi^2 = 6.19$ , d.f. = 1,  $P < 0.01$ ).

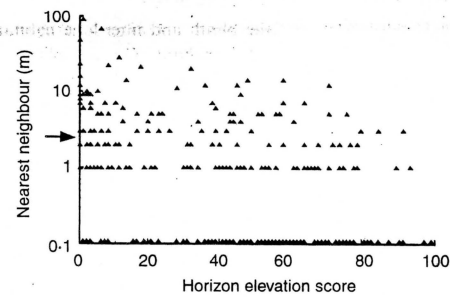


Fig. 4. Nearest neighbour distances (log scale, m) of spider webs vs. the sum of four horizon elevation scores at the site. Remote webs, forming 24% of the total, are located above the arrow.

Of the three web variables (web length, number of capture lobes, lobe width), only web length differed significantly between clustered and remote webs ( $z = 3.3$ ,  $P = 0.0009$ ). Remote webs tended to be smaller.

#### HARUBES SITE

The average density of webs of *S. henscheli* on the star dune at Harubes was  $0.060 \text{ m}^{-2}$  (range 0–0.133  $\text{m}^{-2}$  in 30-m long segments). The dune was more densely vegetated than at Khommabes and was dominated by medium-sized grasses, which were present within 2 m of 97% of the 50 web sites and 14 random, dummy sites. *Seothyra* occurred at all dune levels except on the unstable, steep upper dune. Ants were common in all habitats but the interdune. Slope and horizon decreased, and sand compaction increased, down the dune plinth. There were no significant relationships between spider abundance and slope, compaction, horizon or ant abundance (multiple regression  $r^2 = 0.34$ ,  $P = 0.389$ ; simple regressions were not significant). Slope, compaction and horizon measured at spider web sites and at dummy sites were all correlated positively ( $r > 0.57$ ,  $P < 0.03$ ).

Three PCA axes explained 62% of the variation in nine environmental factors measured at web sites. The first axis loaded most strongly on the northern and western horizon elevation, slope, compaction and medium plants, the second on large and small plants, and the third on the western and southern horizon (Table 3). The main differences with Khommabes were that slope, medium plants and compaction were associated with the first axis and not with later axes.

Web geometry (capture lobe width, number of lobes and web length) did not differ with respect to dune slope, compaction and the nearby horizon elevation ( $r^2 < 0.08$ ,  $P > 0.05$ ). Sand flow was not measured.

Webs were larger at Harubes than at Khommabes (lobe width: medians = 10 vs. 7,  $H = 4.2$ ,  $P < 0.001$ ; web length: medians = 38 vs. 30,  $H = 2.4$ ,  $P = 0.015$ ). The residual web length did not differ between the

two study areas ( $H = 0.2$ ,  $P = 0.85$ ). Thus, web size differences were probably due to differences in spider size rather than different responses to the local conditions.

#### TRANSLOCATION EXPERIMENT

At Khommabes, spider size and web parameters were compared for *S. henscheli* taken from the Hummock region and released in each of the three habitats. The initial measurements of mass, body length, capture lobe width and web length did not differ between the three groups ( $H < 0.58$ ,  $P > 0.7$ ).

The spiders were released on the surface one at a time at dusk and were observed until they constructed a small silk mat and disappeared into the sand beneath it. There was no difference in the time it took spiders to complete this phase in the three habitats (median = 104 s, range 30–257 s; excluding one spider on the plinth that did not spin a web at all). The spiders moved further in settling on the plinth than in other regions ( $z > 1.96$ ,  $P < 0.05$ ), but in all habitats 84% of spiders moved <1 m and the maximum distance was <5 m.

Only three spiders moved from their initial location during the 6 weeks following translocation (one in the hummocks and two in the interdune). Mortality during the 6 weeks was 4.7% in the hummocks, 25.0% on the plinth (comparison with hummocks:  $\chi^2 = 2.92$ , d.f. = 1,  $P > 0.05$ ), and 36.0% in the interdune (comparison with hummocks:  $\chi^2 = 4.72$ , d.f. = 1,  $P < 0.05$ ). Predation was caused by gerbils ( $n = 3$ ) and by araneophagous spiders *Ikuma* sp. (Palpimanidae) ( $n = 4$ ) and *Hermacha* sp. (Cyrtauchenidae) ( $n = 1$ ). Eight *S. henscheli* in the interdune did not become established after building an initial web and died in short burrows that appeared to have been obstructed by gravel.

The webs and spiders (Table 4) that survived and did not move were measured after 6 weeks ( $n = 19$ , 13 and 18 spiders in the hummock, interdune and plinth, respectively). Spiders recaptured on the plinth were significantly smaller than those recaptured in the hummocks, while those in the interdune did not differ significantly from either. Seventy-five per cent of the plinth spiders lost weight, compared with 46% in the interdune and 37% in the hummocks. On average, plinth spiders lost 6% body mass compared with gains of 17% and 21% by interdune and hummock spiders, respectively. Body length measurements showed similar trends. Capture-lobe width, web length, residual web length and burrow depth did not differ significantly.

In all habitats, webs of released spiders had significantly fewer lobes than resident webs in the same habitat ( $F = 8.7$ ,  $P = 0.003$ ). However, a multiple ANOVA with habitat type, week and treatment (translocated vs. resident) as factors was not significant ( $P = 0.37$ ).

Table 4. Test statistics (Kruskal–Wallis  $H$  and Wilcoxon Mann–Whitney  $z$ ) and medians for resident and translocated spiders, measured 6 weeks after the start of the experiment. Bold figures indicate significant differences ( $P < 0.05$ ) between spiders released in the interdune and plinth habitats vs. controls re-released in the hummock habitat

Variable	$H$	$z$			Median	
		Interdune	Plinth	Hummock	Interdune	Plinth
Change by resident spiders						
Lobe width (%)	0.6	0.75	0.06	40	50	27
Web length (%)	<b>7.2</b>	0.64	<b>2.26</b>	20	26	0
Change by translocated spiders						
Mass (%)	<b>6.8</b>	0.83	<b>2.59</b>	13	1	–9
Body length (%)	<b>14.0</b>	0.94	<b>3.67</b>	4	4	–6
Lobe width (%)	1.6	0.73	1.26	0	–9	–11
Web length (%)	3.0	0.92	0.74	–5	–16	–1
Values for translocated spiders						
Mass (mg)	<b>6.3</b>	1.56	<b>2.43</b>	33	42	17
Body length (mm)	<b>6.9</b>	1.50	<b>2.57</b>	7	7	5
Lobe width (mm)	0.9	0.41	0.44	11	9	9
Web length (mm)	1.3	1.12	0.36	38	30	36
Burrow depth (mm)	–	–	1.78	126	–	117

## VARIATION AT TWO SCALES: HABITATS AND WEB SITES

The three major dune habitat types (hummock, interdune and plinth) differed from one another in topography and vegetation. Consequently, average slope, horizon elevation, sand flow and the variance of surface level change (deposition or deflation) all differed significantly among the habitats. Webs of *S. henscheli* were most abundant in the vegetated hummock region and least common on the wind-exposed plinth. Webs were associated most strongly with sites where surface sand flow was low (stable sites). Low sand flow, high horizon elevations and the proximity of vegetation were correlated characters typical of the hummock habitat.

Spiders at stable sites were larger than at sites with high sand flow. This relationship suggests that sand stability is the major factor determining the distribution of *S. henscheli* in the different dune habitats. Another indication of the importance of sand flow is that spiders on the plinth, where there is high sand flow, had lower growth rates than in other habitats. In 6 weeks, most translocated spiders on the plinth did not recover the loss in body mass due to building a new web and burrow, whereas many spiders in the hummocks and interdune had increased in mass by the end of the experiment. The overall smaller size of *S. henscheli* at Khommabes compared to Harubes, 40 km east of Khommabes, is perhaps also related to generally stronger winds and consequently higher sand flow in the western part of the Namib sand sea.

Ant abundance differed among the three habitats. In particular, the smaller *T. rufescens* was rare in the plinth habitat. Juvenile *Seothyra* at dispersal are too small (c. 2 mg) to capture *C. detritus* (c. 24 mg) and may rely on *T. rufescens* (<2 mg) as prey. Thus, low availability of *T. rufescens* may limit the survival of juveniles in the dune-plinth habitat. Both species of dune ants were most common in the Hummock habitat and their abundance correlated with spider abundance. Together, these two ant species constituted 87% of the diet of *S. henscheli* in the dunes (Henschel & Lubin 1992).

Both *T. rufescens* and *C. detritus* are associated with particular vegetation: *C. detritus* forages on honeydew produced by scale insects on perennial grasses (Curtis 1985a,b), and *T. rufescens* is a granivore that is common in grass hummocks (Marsh 1986). In spite of the reliance of these ants on vegetation for their own food, webs of *Seothyra* were not clearly associated with plants. The distances between webs and nearest dune plants did not differ from random. If foraging trails of ants change frequently and the spiders are sedentary (see below), web placement next to particular plants may not be advantageous in the long run.

Translocated spiders suffered higher mortality in

the plinth and interdune habitats than in the hummock habitat. On the plinth, the araneophagous spider *Ikuma* sp. (Palpimanidae) accounted for 67% of the mortality of translocated spiders. This species normally preys on *Carparachne aureoflava* (Heteropodidae) in the plinth habitat (Henschel 1990a). In the interdune, the hard substrate and presence of stones increase the difficulty of burrowing. Spiders that encounter obstructions during burrowing may be unable to complete the burrow in a single night or may not have the energy reserves to dig another (Henschel & Lubin 1992). Burrows need to be >6 cm deep for spiders to survive high daytime temperatures (Lubin & Henschel 1990). Juvenile spiders would experience similar problems at first dispersal, further accounting for the relatively low abundance of *S. henscheli* in the interdune habitat.

On the large scale of habitat type, the abundance of *S. henscheli* is largely explained by features associated with sand flow, temperature, prey and predators. In the hummocks, low or variable sand flow, high prey abundance, low risk of predation, low cost of digging and low risk of desiccation in burrows that are too short have the net result that *Seothyra* webs are more abundant in this habitat than in the plinth or interdune habitats (Table 5). At the scale of the web site, these relationships are less obvious. The distribution pattern of *S. henscheli* webs was clumped. Sometimes, high densities of webs could be found in a small area, while apparently similar areas nearby were vacant. Local variation in spider abundance at the small scale was not explained by variation in any of the physical habitat features measured. Sand flow, the most important factor at the larger scale, did not explain clustering of webs at the scale of the web site.

## WEB SITE TENACITY VS. DISPERSAL

While habitat features did not explain the web sites occupied by *S. henscheli*, they did influence the condition of spiders at the small scale. This is evidenced by the fact that remote spiders (>2 m distant from conspecifics) had smaller residual web lengths than clustered individuals. Positive residuals of a regression of web length on lobe diameter indicate a spider that is in good condition relative to its body size (Lubin & Henschel 1996). Furthermore, at sites with low sand flow, residual web length was positively correlated with ant abundance. Thus, spiders in segments with high ant abundance were in better condition. This latter relationship, as well as an overall positive correlation between spider and ant abundances at the habitat level, suggests that spiders cluster where ant abundance is high.

The clustered distribution observed in *Seothyra* at the small scale could be a consequence of active site choice, differential mortality or local (reduced) dispersal of young. Reduced dispersal in this species may be the main reason for clustering. Dispersing young

Table 5. Summary of factors that appear to determine abundance, condition (growth rate and relative web length) and survival of *S. henscheli* in the hummock, interdune and plinth habitats. Relative scores for habitat quality are: 1 = best; 2 = intermediate; 3 = worst

	Habitat quality		
	Hummocks	Interdune	Plinth
Conditions			
<i>Camponotus</i> abundance	1	3	2
<i>Tetramorium</i> abundance	1	2	3
Sand flow	1-3	1	3
Predation risk	1	1	3
Burrow obstruction	1	3	1
Spider response			
Abundance	1	2	3
Condition	1	2	3
Survival	1	3	2

move only short distances from the maternal burrow, and burrow relocation after this initial dispersal is rare (Henschel & Lubin 1992, and unpublished data). The observation that high-density patches are maintained over successive generations (>7 generations at one site; Henschel & Lubin, unpublished data) is consistent with the interpretation of dispersal over short distances. Furthermore, we observed that excavated and released spiders moved only short distances (generally <1 m) and within minutes began to dig a new burrow (Lubin & Henschel 1990; Henschel & Lubin 1992; present study). We conclude that *Seothyra* normally does not engage in active site choice, but settles and remains near the maternal web site. Reduced dispersal seems to be a common trait in spiders of the family Eresidae (*Eresus niger*: Norgaard 1941; *Stegodyphus*: Ward & Lubin 1993; Henschel, Schneider & Lubin 1995). In contrast, dispersal occurs relatively frequently in some other psammophilous spiders, but there too, the relocation distances are generally short (<1 m; Henschel 1990b; Marshall 1995a,b).

The apparent lack of strong site-selection behaviour may be an adaptive strategy for *S. henscheli*. Relocation is risky because of predators and the risk of desiccation, and building a new web is energetically costly (Henschel & Lubin 1992; Lubin & Henschel 1996). Furthermore, prey availability may be difficult to predict both in space and time. Moving to a new web site in order to improve prey capture is thus both risky and of uncertain value. In another desert spider found in the climatically less extreme Negev desert, prey availability was similarly shown to be an unreliable cue for assessing habitat quality (Lubin *et al.* 1993).

Ellner & Shmida (1981) found that seeds of desert plants disperse over short distances. They reasoned that the chance of finding good sites away from the mother plant is no greater than near it. An outcome

of this dispersal strategy is the re-use of the maternal site, a site that was at least adequate in quality in the previous generation (Zohary 1937). We suggest that this principle is applicable also to *Seothyra* in dune habitats. The longevity of some patches indicates that the quality of such sites may remain similar from year to year and this would favour philopatry of the young.

Nevertheless, dispersal over large distances may occur in *S. henscheli*. Some of the remote webs (nearest neighbour >2 m away) could be spiders that moved further than usual. Remote webs were associated with sites with low horizon elevation. Long-distance dispersers may colonize new dune habitats by crossing interdune plains, provided they can survive and reproduce in this habitat over sufficient generations to reach a more favourable one.

## HABITAT SELECTION VS. TOLERANCE

Predictable changes, such as resource depletion (Charnov, Orians & Hyatt 1976), normally do not play an important role in movement decisions of web spiders, where changes in resources occur independently of the spiders' presence (Janetos 1986). This is undoubtedly true of dune habitats, where prey and physical conditions are not predictable in the short term. Thus, for *Seothyra*, the ability to tolerate a wide range of habitat conditions should be more important than active habitat selection.

*Seothyra henscheli* adapts to local conditions by adjusting its web geometry and activity. When wind-blown sand frequently reduces the prey-trapping function of the web, spiders tend to reduce the number of capture lobes that they maintain and save on metabolic costs of activity (Henschel & Lubin 1992). Hungry spiders increase the number of capture lobes and foraging effort in order to improve foraging returns (Lubin & Henschel 1996). Food supplementation and deprivation experiments revealed that spiders in the

hummock habitat were generally hungry (Lubin & Henschel 1996). Their average daily food consumption was equivalent to only 0.66% of their own body mass, which is considerably less than 2.08% of body mass at the maximal growth rate. Conditions would be even less favourable in other habitats. In the present census at Khommabes, 85% of the population was foraging on the day of the census, again suggesting most spiders were hungry.

Given the constraints on activity and web-renewal placed by wind-induced sand flow and the high costs of moving to a new site, *S. henscheli* may have little choice but to adapt its growth strategy to conditions available at the current web site. Spiders at poor web sites have smaller residual web lengths and lower body mass. Site-dependent growth can have far-reaching effects on lifetime fitness in these annual spiders: spiders in poor condition may reproduce later and will have fewer offspring than spiders in good condition (Lubin & Henschel 1996).

In conclusion, we suggest that the variation in abundance of *S. henscheli* in the different habitats is a consequence of (i) philopatry at the small scale combined with (ii) differential growth and mortality in different habitats. Among the species of *Seothyra* in southern Africa, *S. henscheli* has one of the widest distributions; many other species are restricted to small sand-dune 'islands' (Dippenaar 1990), further supporting the idea of strong philopatry in the genus as a whole. It is interesting to consider, therefore, how *S. henscheli* populations might have spread and become established in new areas. Our current studies of population changes in two Namib dune sites show that populations can increase rapidly when they encounter favourable areas, suggesting a high intrinsic rate of growth in this species. Thus, although *S. henscheli* may be a conservative disperser with a site-dependent growth strategy, it is also a successful invading species. This combination of conservative dispersal and large reproductive potential may explain the success of this species in the spatially variable and temporally unpredictable environment of the Namib sand sea.

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