Psammophily in Namib Desert spiders

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A community of psammophilous spiders was studied in the central Namib Desert. Of 20 species, 85% were cursorial. Complex setae, claws or keels facilitate digging, sweeping, carrying, and swimming in or walking on sand, while long spigots enable spiders to bind sand with silk when burrowing down to depths with amenable microclimate (10–120 cm). Sand is excavated either by sweeping it up an incline or carrying it vertically up. Other characteristics of dune spiders were large size, polyphagy, low metabolism, longevity, brood care and seasonal foraging and breeding patterns. The large, dominant heteropodid, Leucorchestris, may determine many characteristics of the Namib arthropod community.

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Introduction

Sand is an important substrate in the Namib Desert. Its important characteristics from an ecological perspective (Seely, 1991) are its granular structure, the shifting nature of the surface, the relative lack of shelter on the surface, and its relative ease of penetration. Extreme and hostile microclimatic conditions often prevail on the surface (high temperature, low humidity, sand abrasion) but below there is a gradient of variable temperatures and humidity that arthropods can choose. Food is obtained typically on or near the surface, and shelter below it. Psammophily—living in sand—and, in particular, ultrapsammophily—specialization to sandy substrata—often involves special morphological and behavioural characteristics that enable animals to burrow into and move across the sand efficiently (Cloudsley-Thompson, 1991).

A wide diversity of psammophilous animals exploit the Namib Desert dunes. Well-known examples are tenebrionid beetles (Koch, 1962; Coineau et al., 1982; Seely, 1983), Thysanura (Watson & Irish, 1988), scorpions (Lamoral, 1979), gerbils (Griffin, 1990), golden moles (Fielden, 1991), snakes (Robinson & Hughes, 1978), geckos (Bauer & Russell, 1991) and lizards (Robinson, 1990).

In this paper, psammophily is described in spiders of the Namib Desert. I dedicate it to Professor John Cloudsley-Thompson, who knows the Namib (e.g. Cloudsley-Thompson, 1990a, b) and desert spiders (Cloudsley-Thompson, 1967, 1975, 1978, 1982, 1983, 1984, 1986, 1987, 1988, 1990a, 1991, 1993). According to him, some of
the important characteristics of desert spiders are that they tend to be wandering hunters rather than web-builders, often detect their prey via substrate vibrations, are polyphagous, and can tolerate long periods without food due to low metabolism. Desert spiders tend to be large, long-lived (> 2 years), nocturnally active, often have brood care and use burrows as retreats. Many of them have tarsal scopulae to walk on sand and to brush it out of the burrows. Coloration tends to be pale or cryptic. Their ecophysiological characteristics include efficient excretion, discontinuous respiratory cycles, and heat tolerance.

The natural history and some behavioural and morphological aspects of various psammophilous spiders of the Namib have been described before (e.g. Lawrence, 1962, 1965a, b, 1966; Henschel, 1990a, b, 1994; Platnick & Griffin, 1990; Lubin & Henschel, 1990, 1996; Henschel & Lubin, 1992, 1997; Peters, 1992a, b; Turner et al., 1993; Roth & Roth, 1996; Lubin et al., submitted), and Griffin & Dippenaar-Schoeman (1991) gave a checklist of the published spider fauna of the central Namib. Here, I derive some general patterns for Namib dune spiders based on my observations and published accounts. The broad question that I examine concerns whether sand-dwelling spiders possess special features that are peculiar for their occurrence in sandy habitats and differ from those of spiders in other habitats. These questions are addressed for spiders of the Namib Desert dunes, in a description of aspects of their general morphology, natural history, burrow structure and community ecology, that appear to be important for their existence in sand.

Study area

The study area was located in the northern part (20 × 130 km) of the Greater Sand Sea of the central Namib Desert. The area encompassed the width of the sand sea from the southern bank of the Kuiseb River, excluding the riverbed, to 30 km south (23°20′-24°00′S, 14°30′-15°50′E). The three principal study sites were: (1) Sandwich Bay (23°22′S, 14°30′E) along the west coast in transverse dunes of <100 m height; (2) south of Gobabeb (23°34′S, 15°02′E), 30-80 km from the coast, on linear dunes of 50-200 m height or on 1-km wide interdune plains; and (3) the eastern dunes, 100-130 km from the coast between Harubes, Tsoneb Vale and Far East (23°40′-24°00′S, 15°20′-50′E), on the relatively richly vegetated slopes of star and reticular dunes. The main study sites within a 30 km radius of Gobabeb were Visnara, Obartaem, Khommabes, Khubab, Kahani, J-line and Noctivaga. The relative proportions of different dune habitats were (Seely & Louw, 1980): 55% interdune plains, 32% lower plinth and 13% upper slope (leeward) and slipface. Fossil burrows were located on the Diewrivier farm (24°07′S, 15°52′S). Voucher specimens of spiders are deposited at the National Museum of Namibia, Windhoek, while fossils are with the Geological Survey of Namibia, Windhoek.

Methods

Fieldwork was conducted between 1986 and 1996, during which period the study sites were visited on numerous occasions. Tracks and burrow entrances of dune spiders are clearly visible after sunrise following a relatively calm night (Henschel, 1990b). Spiders were captured when active on the surface, or by excavation, or with spider traps (Henschel, 1991). Non-psammophilous spiders were also recorded in the dunefield, but some species living among rocks in the interdune valleys may have been overlooked as this habitat was not studied intensively.
Results & discussion

Dune fauna

Twenty species from 10 families of psammophilous spiders were found in the Namib dunes (Table 1). The community was dominated by wandering spiders in terms of diversity, abundance and biomass. Only one Mygalomorph (Nemisiidae) and three web spiders occurred (Eresidae, Theridiidae and Segestriidae). Overall, the Heteropodidae, Leuchoristis, Carparachne and Orchestrella, were most widespread in each habitat and appeared to dominate. Locally, the eresid, Seothyra, the gnaphosid, Asemesthes, the ammoxenid, Rastella, and the zodariid, Psammoduon, could be abundant.

Twelve of the 16 identified species are endemic to the central Namib, nine being confined to the Greater Sand Sea. The local species richness was lowest at Sandwich Bay (6), increasing eastwards (15) (Table 1). By habitat, species richness was highest (11) on the lower plinth and dune base, and lower on the interdune (6) and upper plinth and slipface (6).

The non-psammophilous spider community living on or under plants or stones in the Namib dunefield comprised 12 species from 10 families (Table 2). These spiders were generally rare or uncommon, except for Sicarius (Sicariidae) and Hirriusa (Philodromidae) that occurred under stones and on perennial grass, respectively. These spiders generally had a wider distribution in Namibia and some may not sustain viable populations in the dunefield. Cosmophasis (Salticidae) mimics the dune ant Camponotus dertius, but lives on the grass or in ant nests (Curtis, 1988). The fairly common Sicarius albospinosus requires loose sand to bury itself (Reiskind, 1965, 1969), but it is not grouped among the psammophilous spiders because of its dependence on shade under stones and plants.

Several taxonomic problems were encountered with the psammophilous spiders. Ariadna sp. (Segestriidae) appears to be undescribed. The salticids could not be identified. The 'wheeling salticid' was the most common kind: the female was pale with a light stripe over the middle of the opisthosoma, while the male had a brown carapace with a pale patch median-posteriorly, and a thick, dark brown stripe over the middle of the opisthosoma, with both sexes having lightly striped legs and tarsal tufts. Suseoda (Theridiidae) was probably S. capensis, but this requires confirmation when adults are collected. The immature Rastella was possibly R. sabulosus (Platnick & Griffin, 1990) or an undescribed species (Roth & Roth, 1996). The red sand-coloured Asemesthes sp. A (referred to as Asemesthes in the remaining sections) was the most common morphotype in the dunes, while some six more morphotypes are conservatively designated as Asemesthes sp. B (Table 1). The large Asemesthes species complex in Namibia begs systematic analyses (Platnick, pers. comm.). Until the Namib Heteropodidae are formally revised, I suggest the following synonymies, based on my field observations: Leuchoristis arenicola (L. kochi (see Henschel, 1990b)); Orchestrella longipes (O. browni (O. caroli are sympatric with various life stages and sexes resembling one or the other species designated by Lawrence (1962, 1965a, 1966), O. longipes being used here); Carparachne alba and C. aureoflava are sympatric and virtually indistinguishable except by colour (the slight differentiation of eye arrangements recognized by Lawrence (1966) is a continuum), but are kept separate here because of the colour difference.

Characteristics of psammophily

Among the psammophilous spiders there is a steady progression of increasing body length between Rastella (2 mm) and Leuchoristis (25 mm) (Fig. 1). A similar trend
<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
<th>A*</th>
<th>Level †</th>
<th>Place ‡</th>
<th>Position §</th>
<th>Body length (mm) ††</th>
<th>Burrow length (cm) ††</th>
<th>Burrow depth (cm) ††</th>
<th>Burrow slope (°) ††</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nemesiidae</td>
<td><em>Hermachia lanata</em> Purcell, 1902</td>
<td>4</td>
<td>I,L</td>
<td>G,E</td>
<td>b</td>
<td>20 (14-28)</td>
<td>115 (61-168)</td>
<td>80 (25-120)</td>
<td>44 (30-58)</td>
</tr>
<tr>
<td>Segestriidae</td>
<td>Ariadna sp.</td>
<td>3</td>
<td>L</td>
<td>G,E</td>
<td>b</td>
<td>9 (7-11)</td>
<td>24 (10-32)</td>
<td>24 (10-32)</td>
<td>90</td>
</tr>
<tr>
<td>Palpimanidae</td>
<td><em>Diaphrocelus buplaga</em> Simon, 1893</td>
<td>1</td>
<td>L</td>
<td>G</td>
<td>a</td>
<td>6 (5-7)</td>
<td>11 (10-12)</td>
<td>11 (10-12)</td>
<td>90</td>
</tr>
<tr>
<td>Palpimanus</td>
<td><em>stridulator</em> Lawrence, 1962</td>
<td>3</td>
<td>U</td>
<td>G,E</td>
<td>s</td>
<td>17 (10-12)</td>
<td>12 (6-18)</td>
<td>12 (6-18)</td>
<td>90</td>
</tr>
<tr>
<td>Eresidae</td>
<td><em>Seothyra henscheil</em> Dippenaar-Schoeman, 1990</td>
<td>4</td>
<td>L</td>
<td>S,G,E</td>
<td>b</td>
<td>7 (4-12)</td>
<td>12 (6-18)</td>
<td>12 (6-18)</td>
<td>90</td>
</tr>
<tr>
<td>Theridiidae</td>
<td><em>Steatoda</em> sp.</td>
<td>2</td>
<td>L</td>
<td>E</td>
<td>b</td>
<td>4 (3-4)</td>
<td>7</td>
<td>7</td>
<td>90</td>
</tr>
<tr>
<td>Zodariidae</td>
<td><em>Psammoecus deserticola</em> (Simon, 1910)</td>
<td>4</td>
<td>U,L</td>
<td>S,G,E</td>
<td>s</td>
<td>9 (7-11)</td>
<td>14 (10-17)</td>
<td>14 (10-17)</td>
<td>90</td>
</tr>
<tr>
<td>Diores triangularis Simon, 1910</td>
<td>2</td>
<td>I</td>
<td>E</td>
<td>s</td>
<td>5 (5-6)</td>
<td>7</td>
<td>7</td>
<td>90</td>
<td></td>
</tr>
<tr>
<td>Psammorymga caligata Jocqué, 1991</td>
<td>2</td>
<td>I</td>
<td>E</td>
<td>b</td>
<td>14 (10-17)</td>
<td>8 (6-10)</td>
<td>9 (6-10)</td>
<td>90</td>
<td></td>
</tr>
<tr>
<td>Ammoxenidae</td>
<td><em>Ammoxenus coccineus</em> Simon, 1892</td>
<td>1</td>
<td>I</td>
<td>G,E</td>
<td>a</td>
<td>3</td>
<td>14 (10-17)</td>
<td>14 (10-17)</td>
<td>90</td>
</tr>
<tr>
<td>Rastellus sabulosus Platnick &amp; Griffin, 1990</td>
<td>4</td>
<td>L</td>
<td>G,E</td>
<td>b</td>
<td>1 (1-3)</td>
<td>8 (6-10)</td>
<td>9 (6-10)</td>
<td>90</td>
<td></td>
</tr>
<tr>
<td>Gnaphosidae</td>
<td><em>Asemethes</em> sp. A</td>
<td>4</td>
<td>I,L,U</td>
<td>G,E</td>
<td>b</td>
<td>6 (5-7)</td>
<td>15 (6-29)</td>
<td>15 (5-17)</td>
<td>21 (11-26)</td>
</tr>
<tr>
<td>Asmethes sp. B</td>
<td>3</td>
<td>I</td>
<td>G</td>
<td>b</td>
<td>6 (4-7)</td>
<td>14 (10-17)</td>
<td>14 (10-17)</td>
<td>90</td>
<td></td>
</tr>
<tr>
<td>Camellina corrugata (Purcell, 1907)</td>
<td>1</td>
<td>L</td>
<td>S</td>
<td>a</td>
<td>7 (6-9)</td>
<td>7</td>
<td>7</td>
<td>90</td>
<td></td>
</tr>
<tr>
<td>Heteropodidae</td>
<td><em>Leuorchestris arenicola</em> Lawrence, 1962</td>
<td>5</td>
<td>L</td>
<td>G,E</td>
<td>b</td>
<td>25 (16-32)</td>
<td>36 (12-100)</td>
<td>22 (9-67)</td>
<td>29 (16-33)</td>
</tr>
<tr>
<td>Carparachne aureoflava Lawrence, 1966</td>
<td>5</td>
<td>U</td>
<td>S,G,E</td>
<td>b</td>
<td>12 (10-20)</td>
<td>51 (6-122)</td>
<td>38 (6-65)</td>
<td>19 (8-29)</td>
<td></td>
</tr>
<tr>
<td>Carparachne alba Lawrence, 1962</td>
<td>3</td>
<td>U</td>
<td>S,G,E</td>
<td>b</td>
<td>15 (11-21)</td>
<td>49 (23-81)</td>
<td>36 (20-55)</td>
<td>21 (14-29)</td>
<td></td>
</tr>
<tr>
<td>Orchestrella longipes Lawrence, 1965</td>
<td>4</td>
<td>I</td>
<td>G</td>
<td>b</td>
<td>18 (17-19)</td>
<td>[20-40]</td>
<td>[15-30]</td>
<td>[25]</td>
<td></td>
</tr>
<tr>
<td>Microorchestris melanolabis Lawrence, 1962</td>
<td>1</td>
<td>U</td>
<td>S</td>
<td>b</td>
<td>10</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Salticidae</td>
<td>unknown ('wheeling salticid')</td>
<td>4</td>
<td>I,L</td>
<td>G,E</td>
<td>b,a</td>
<td>4 (3-4)</td>
<td>[10]</td>
<td>[10]</td>
<td>[25]</td>
</tr>
</tbody>
</table>

*Classes of relative abundance range from 1 (=present) to 5 (=abundant).
†Codes for dune level are: I=interdune; L=lower plinth and base; U=upper plinth, slipface and crest.
‡Places are: S=Sandwich Bay; G=Gobabeb; E=eastern dunes.
§Position is: b=burrow; s=sand-swim; a=active on surface.
††Dimensions indicate averages, ranges in parentheses and estimated values in square brackets.
Table 2. Non-burrowing spiders associated with perennial vegetation or stones in the central Namib dunes.
The position on or under the vegetation or stones is indicated.

<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
<th>A</th>
<th>Position</th>
<th>Body length (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sicariidae</td>
<td>Sicarius albospinosus Purcell, 1908</td>
<td>3</td>
<td>Beneath</td>
<td>8</td>
</tr>
<tr>
<td>Caponiidae</td>
<td>Doplogena capensis Purcell, 1904</td>
<td>1</td>
<td>Beneath</td>
<td>9</td>
</tr>
<tr>
<td>Eresidae</td>
<td>Gandanomena echinatus (Purcell, 1908)</td>
<td>2</td>
<td>Against stem</td>
<td>15</td>
</tr>
<tr>
<td>Theridiidae</td>
<td>Latrodectus cinctus Blackwall, 1865</td>
<td>2</td>
<td>Under overhang</td>
<td>13</td>
</tr>
<tr>
<td>Araneidae</td>
<td>Argiope nigrommata Thorell, 1859</td>
<td>1</td>
<td>Web in canopy</td>
<td>18</td>
</tr>
<tr>
<td>Oxyopidae</td>
<td>Peuceta viridis (Blackwall, 1858)</td>
<td>1</td>
<td>Web in canopy</td>
<td>13</td>
</tr>
<tr>
<td>Clubionidae</td>
<td>Clubiona sp.</td>
<td>1</td>
<td>Retreat on stem</td>
<td>5</td>
</tr>
<tr>
<td>Philodromidae</td>
<td>Hirriusa bidentatus (Lawrence, 1927)</td>
<td>3</td>
<td>Wander on plant</td>
<td>4</td>
</tr>
<tr>
<td>Thomisidae</td>
<td>Thomisus sp.</td>
<td>2</td>
<td>Wander on plant</td>
<td>4</td>
</tr>
<tr>
<td>Salticidae</td>
<td>Cosmophasis sp.</td>
<td>2</td>
<td>Wander on plant</td>
<td>7</td>
</tr>
</tbody>
</table>

A=abundance; see Table 1 for explanation.
was evident for the non-psammophilous dune spiders, although the largest spider was somewhat smaller than *Leucorchestris*. The size distributions in the psammophilous and non-psammophilous groups did not differ from each other (Mann-Whitney $U = 112.5, p > 0.05$), but both differed from a non-desert community of 38 species of spiders in a nettle-field near Würzburg in southern Germany ($U$-psammophilous $= 860$, $U$-non-psammophilous $= 432, p < 0.001$). Whereas 70% of the Namib spiders were larger than 5 mm, only 20% of the spiders from Germany fell into this class. This supports the hypothesis that Namib dune spiders, whether psammophilous or not, tend to be large, but that psammophily per se does not appear to affect size.

Highly-developed tarsal scopulae, complex adhesive hairs and tarsal tufts are characteristic of the heteropodids, palpimanids and salticids. These evidently facilitate walking on sand. Gnaphosids have smaller tarsal tufts. For digging, these families and zodariids have complex and strong setae, spines and claws on the legs and pedipalps. These are well-developed on the legs of *Psammoduon* (Jocqué, 1990). In *Rastellus*, the setae on the anterior tip of the chelicerae are modified rastelliform for digging (Platnick & Griffin, 1990), while *Seothyra* has a strong chitinous keel on the anterior margin of the cheliceral groove (Dippenaar-Schoeman, 1990) that may serve the same purpose.

Most (70%) spiders lived in burrows (Table 1), of which all had a trap-door, collar-door or silken screen over the entrance. In only one spider, *Psammorygma caligata*, did the burrow entrance protrude upwards as a turret of several centimetres in height. Some spiders (*Hermacha, Ariadna*) had loose, silken collars along the length of the burrow. Voluntary sand-swimming was recorded in only three species (*Psammoduon, Diores, Palpimanus*), although other spiders could wriggle through the sand if their burrows collapsed. *Psammoduon* spins a silk-lined cell in the sand to moult or deposit and guard its egg cocoon, while *Palpimanus* takes over the burrow of its spider prey.

Spider burrows were at least deep enough to penetrate beyond the critically hot layer, the top 6 cm of sand that gets hotter than 49°C during summer afternoons (Lubin & Henschel, 1990). Some individuals of several species scarcely dug deeper than that, indicative of heat tolerance (Table 1). Nearly all species, however, usually burrowed to depths exceeding 10 cm and 50% dug deeper than 20 cm, where the daily temperature fluctuations are only about 2°C compared to >40°C at the surface (Lancaster et al., 1984). At the depths of 25–120 cm to which *Carparachne* and *Hermacha* burrow, only minor temperature changes are experienced on a seasonal

Figure 1. Size distribution of psammophilous spiders (●), non-psammophilous dune spiders (□), and of a European spider community (▲).
basis. The thermophilous spider, Seothyra, that has a critical thermal maximum of 49°C, uses the thermal gradient at the surface to its advantage. It captures prey during the heat of the day, shuttling up and down between the 60–70°C hot web and the 35°C cool bottom of its burrow (Lubin & Henschel, 1990; Turner et al., 1993). The diurnally active Asemesthes appears to use similar shuttling behaviour to remain below its critical thermal maximum.

Psammophilous spiders had two major types of burrows, sloping either vertically down, or at a gradual angle. Dry dune sand has a maximum surface angle of inclination of 32° (Robinson & Seely, 1980). Animals that dig by sweeping sand from their excavations cannot construct burrows at steeper angles, whereas animals that carry sand out of excavations can dig steeper, provided the sand is stabilized. Namib spiders use both techniques, 50% of them sweep and 50% carry. The burrows of sweepers were usually inclined between 19 and 29° (Table 1). Carriers dug vertically down, except Hermacha, which dug at an unusual angle of 30–58° into consolidated sand. Carriers evidently bound the sand parcels with silk, probably to facilitate carrying. The silk-sand bundles were either spun onto the surface webbing (Seothyra; Peters, 1992a), or were heaped over the burrow entrance (Hermacha, Staatoda, Rastellus), or scattered on the nearby surface (Ariadna, Seothyra).

The burrowing spiders have long spinnerets with very long spigots (observed for heteropodids, Seothyra, Hermacha, and Asemesthes; Peters, 1992a; pers. obs.) that the spiders use to bind the burrow walls. For instance, Leucorchestris stabilizes its burrow wall with a ring of silken nodules that is made by pushing the very long spigots far into the sand to interweave the sand grains (Peters, 1992a). The silken nodules project 2–3 mm into the sand beyond the burrow wall, corresponding to about 10% of the spider's body length. A progression of nodule rings runs along the length of the burrow wall (Henschel, 1990b). This pattern appears to be similar in the burrow-walls of several other spiders (huntsmen, Seothyra, Ariadna), judging by the succession of rings along the burrow. The burrow walls, although not rigid, stabilize the burrows to such an extent that they are functional even in the loose sand of the slip face (Carparachne), although the micro-mechanics are not understood. The investment in silk by individual spiders appears to be very high, but this has only been examined for Seothyra, which requires 6% of its body mass on the first night of burrow construction (Henschel & Lubin, 1992) and probably at least twice as much until the web is functional. The burrows do not deteriorate in undisturbed sand, but there is no evidence of reuse. I have found three fossilized burrows with walls that resemble those of Leucorchestris in Tsondab sandstone, which were formed between 55 and 5 Myr ago (Ward et al., 1983).

Silk may play a role in water acquisition. On foggy mornings, Leucorchestris spiderlings and Seothyra were clinging to the fog-wetted surface silk (trap-door or web) when this was lifted for inspection. Perhaps these spiders drink fog water, using the woven silk as a sponge.

Movements of sand by wind affect the top of the burrow, but this has only been examined for Seothyra (Henschel & Lubin, 1992). Its web remains functional despite regular inundation with sand because the rounded sand grains do not snag in the cribellar silk and the spider can shake them off. Storm winds can, however, cause the loss of Seothyra webs, a condition from which spiders may not recover.

Several spiders make use of Rayleigh waves that moving prey generate on the smooth, continuous sand surface (Brownell, 1977; Brownell & Farley, 1979). Huntsmen can detect these at distances of > 2 m (Henschel, 1990b, 1994). Ariadna may perhaps also detect these waves for foraging, as this spider does not construct trip-lines that are typical for segestriids (Beatty, 1970), but merely monitors the burrow collar that is flush with the sand surface. This method of prey detection via the substratum parallels that of another Namib Ariadna of the gravel plains that uses stones for prey detection (Henschel, 1995). The araneophagous Palpimanus may
generate such Rayleigh waves in order to lure *Carparachne* and *Seothyra* towards it, probably, as observations indicate, by using its extraordinarily-shaped front legs with articulate tarsae.

Another consequence of the smooth, bare sand is that spiders cannot conceal themselves when confronted by predators. Heteropodids use aggression as a deterrent. *Carparachne* and the 'wheeling salticid' transform their bodies and legs into rotating disks to escape by wheeling (Henschel, 1990a). This is only possible on a smooth surface. Navigation is another problem on the featureless surface. Adult male *Leucorchestris* (Henschel, 1990a) and *Carparachne* navigate over long distances (20–450 m) on bare dune surfaces without the use of visual aids or draglines, probably using kinesthetic orientation.

**Ecology and life history**

Different huntsmen tended to use different dune habits. *Leucorchestris* was dominant on the lower plinths of dunes that covered 32% of the dunefield south of Gobabeb (Seely & Louw, 1980). This spider was strongly territorial, with nearest neighbour distances of 4 m in high-density populations of 240 individuals ha\(^{-1}\) (range 9–302 ha\(^{-1}\), Henschel, 1990b). *Carparachne* occupied the slipface at densities of 11–1776 ha\(^{-1}\) (Henschel, 1990a). The interdune valleys contained a relatively sparse population of *Orchestrella*. All other common psammophilous spiders (*Seothyra*, *Hermacha*, *Asemesthes*, *Psammoduon*, *Rastellus*) had a more patchy distribution, with high density patches separated by sparsely- or unoccupied areas. The highest densities were achieved by *Seothyra* that had clusters of 50 m\(^2\) and patches of 100–200 m\(^2\) containing several thousand individuals (Henschel & Lubin, 1997). They lived so close next to each other that conspecifics experienced shadow competition for ants (Lubin et al., submitted). The clustering appeared to be due to the short dispersal distances (<1 m) of juveniles and has profound effects on the population (D. Eisinger, pers. comm.).

Most spider species were polyphagous and tended to concentrate on insects that were slightly smaller than themselves, e.g. 10–30-mm long huntsmen and *Hermacha* fed mainly on 5–20-mm long tenebrionids (Henschel, 1994). *Seothyra* predominantly captured ants, progressing from small *Tetramorium* to larger *Camponotus* as the spiders grew (Henschel & Lubin, 1992). *Asemesthes* was capable of capturing *Camponotus detritus* ants that were over four times the spider's mass (e.g. a 24 mg *Asemesthes* captured a 104 mg ant). *Psammoduon* prey on soft-skinned, sand-swimming insects such as tenebrionid and lepidopteran larvae, and *Thysanura* which they hunt below the sand and on the surface (pers. obs.; R. Rössl, pers. comm.). *Rastellus* is possibly the only stenophagous spider, feeding on *Psamnotermes allocerus* (Rhinotermitidae), similar to other termite-specializing ammoxenids elsewhere (Wilson & Clark, 1977; Dippenaar & Meyer, 1980). *Rastellus* burrows were sometimes very closely (possibly even directly) connected to the termite tunnels, possibly indicating that the spiders captured termites in their burrows.

Araneophagy, including cannibalism, was recorded for the Heteropodidae, Gnaphosidae, Zodariidae and Palpimanidae. *Palpimanus stridulator* specialized in capturing *Carparachne aureoflava* (N = 7) and *Seothyra henscheli* (N = 8). *Leucorchestris* captured any smaller spiders that were active in their territories at night (Henschel, 1990b). They were kleptoparasites and possibly predators of *Seothyra* when these captured prey at night. Similarly, *Asemesthes* attacked other small spiders moving on the surface by day.

Several predators may affect the spider populations. Three different pompilid wasps are parasitoids to three different huntsmen. *Carparachne* is under intensive pressure by the wasps *Schistonyx aterrimus* (N = 42; Henschel, 1990a), while *Leucorchestris* has *S. simiatus* to contend with (N = 4), and *Orchestrella* has *Paxacyphononyx trichriocephalus*
(\(N = 4\)). The gerbil, *Gerbillurus paeba*, was a major predator of *Leucorchestris*, digging it out of its burrow (\(N = 253\); Henschel, 1990b).

Indications are that the Namib spiders have a low metabolic rate, one-quarter that of comparable spiders in other deserts (Henschel, 1994; Lubin & Henschel, 1996). *Seothyra* daily consume the equivalent of 1% of their body mass, and *Leucorchestris* 0.7%. Both species need to obtain a major meal every 5–6 weeks during their main foraging season when they are active for over 50% of the time. *Seothyra* are usually hungry and spend increasingly more foraging effort with progressive hunger in their attempts to improve their foraging returns, but many die of starvation (Henschel & Lubin, 1992; Lubin & Henschel, 1996).

Foraging and breeding tended to be seasonal and need not coincide. *Seothyra* foraged mainly from October to April (summer), and reproduced during winter when storm winds prevented them from foraging (Henschel & Lubin, 1992). *Asemesthes* may follow a similar pattern, and > 50% of the population are adult during April each year. *Leucorchestris* foraged and reproduced during the entire summer and reduced activity during winter (Henschel, 1990b), a pattern that was followed by other huntsmen. *Hermacha* had a different pattern; they foraged and mated during winter sand-storms and reproduced in summer. In *Psammorygma*, reproductive activity was stimulated by rainfall. A rainfall of 10 mm was once followed within hours by the eruption of numerous *Psammorygma* males (\(c. 20 \text{ha}^{-1}\)) in a familiar study area where this species was not seen before. The males searched for females, and guarded them in their burrows.

Extended brood care is seen in at least five spiders (*Leucorchestris*, *Carparachne*, *Seothyra*, *Hermacha*, 'wheeling salticid'), while little information exists for the others. The only two species for which the breeding pattern is known differ: *Seothyra* is semelparous with matriphagous young, and *Leucorchestris* is iteroparous with cannibalistic young. *Seothyra* usually have a life-span of 1 year, which they can extend for a full second year up to the next breeding season (Henschel & Lubin, 1992). Based on field and laboratory observations, several other spiders are known to live longer than 3 years: *Leucorchestris* (Henschel, 1990b), *Carparachne* and *Hermacha* (pers. obs.). An *Ariadna* sp. from the gravel plains has an estimated life-span of 7 years (Henschel, 1995).

**General discussion**

The habitats of the Namib dunes are clearly defined by their physical parameters, which are consistent over space and time (Robinson & Seely, 1980). Given the old age of the Namib, some 80 Myr (Ward *et al.*, 1983), it is not surprising that spiders have had the time for specialization. Most (75%) of the psammophilous spiders of the central Namib are endemic, with 56% being confined to the Great Sand Sea. At least three species are ultrapsammophilous (*Carparachne aureoflava*, *C. alba*, and *Psammo- duon deserticola*) and occur in the most extreme dune conditions, steeply sloping, unconsolidated sand. Several others, such as *Seothyra henscheli*, *Asemesthes* sp. A, and *Leucorchestris arenicola*, are compulsory psammophiles that are absent or very rare in non-sandy substrata. This may also apply to *Ariadna* sp., *Palpimanus stridulator*, and *Rastellus sabulosus*, but not enough is known about these species.

The spider burrow represents an amenable microclimatic haven, where temperature is tolerable away from the hot surface (Seely & Mitchell, 1987), and where the atmosphere gains water vapour so that the spider exists in a non-desiccating environment (Louw, 1993). This is due to vapour pressure differences that result from the temperature gradient (Edney, 1977). Despite this, several Namib spiders are heat-
tolerant (heteropodids, zodariids) or thermophilous (Seothyra, Asemesthes). The latter apply heat to their advantage in capturing prey, and use the microclimatic gradient of the burrow to remain below the critical thermal maximum.

The current study confirmed that desert spiders tend to be larger than other spiders (Cloudsley-Thompson, 1982). Large spiders have a reduced surface-to-volume ratio, decreasing cuticular water loss. Large size may also be of advantage in tackling the heavily sclerotised tenebrionids that form the bulk of the prey of many Namib spiders (Henschel, 1994; pers. obs.), as well as deterring intraguild predators (Polis & McCormick, 1986). Some, but not all Namib spiders are long-lived, while all studied species appear to have brood care, although some species are semelparous (e.g. Seothyra) and others iteroparous (e.g. Leucorchestris). Although no spider appears to have a season of complete inactivity, all were seasonal in their main foraging and breeding activity. Seasonality, although not pronounced in terms of temperature above-ground, may be influenced by the seasonal changes of the temperature regime in the upper layers of sand (Lancaster et al., 1984). Low metabolism may be a crucial feature of Namib spiders (although known for only two species), enabling them to survive long periods of want. This would be of advantage in a desert that has the lowest reported productivity of any terrestrial ecosystem (Seely & Louw, 1980) and is therefore a common feature among Namib arthropods and small vertebrates (Robertson et al., submitted).

Several factors may influence habitat use by dune spiders. Physical factors, such as the degree of sand compaction, slope, exposure of the surface to wind, and the presence of perennial vegetation, can have pronounced effects (Henschel & Lubin, 1997). This is mediated by the spider's ability to tolerate or utilize these characteristics, such as effective use of the smooth surface for wheeling locomotion by Carparachne (Henschel, 1990a). Araneophagous predators are capable of excavating spiders from the sand (e.g. Henschel, 1990a,b; Henschel & Lubin, 1992), while surface-active spiders may detect them via ground-borne vibrations. In the absence of shelter on the dune surface, huntsmen use aggression to deter predators on the surface (Henschel, 1990b).

Intraguild predation between huntsmen may further influence the spatial and temporal distribution of spiders. The largest and fastest-growing huntsman, Leucorchestris (adult mass 1.7–5.0 g), occupies the lower plinth. By monitoring surface vibrations, a population of Leucorchestris can cover the entire surface with contiguous territories. This aggressive and araneophagous spider (also of other spider families) may confine the two smaller huntsmen, Carparachne and Orchestrella, to the upper plinth and the interdune, respectively (Henschel, 1994). Alternatively, the three genera have different capabilities of using the different habitats. The slipface is the most prey-rich habitat of the Namib dunes (Seely & Louw, 1980), but requires a high degree of specialization to sand that only Carparachne has developed. The interdune plains have many stones among the consolidated sand, and perhaps only Orchestrella can dig there.

The overall pattern, however, suggests that Leucorchestris arenicola is a dominant species (in the sense defined by Power et al., 1996) that shapes the rest of the community (Polis & McCormick, 1986). Not only can Leucorchestris exclude other huntsmen from its favoured habitat, but it may possibly also influence the activity period of other species, such as Asemesthes (and tenebrionids), to be diurnal, or Hermacha to be active during winter sand storms when Leucorchestris has reduced activity. Intraguild predation by huntsmen may perhaps also explain the absence of wolf spiders, Lycosidae, in the Namib dunes, despite their presence in the sand of the adjacent Kuiseb riverbed. Lycosids are a major component in many epigaeic spider communities elsewhere, including other deserts (Humphreys, 1976; Wise, 1993; Marshall, 1995; pers. obs.). In the Namib, huntsmen are, however, the larger and more aggressive cursorial predators and may exclude lycosids.
Sand influences Namib spiders in numerous ways, enabling them to establish an amenable microclimate in a harsh environment. Spiders have evolved specialized morphological and behavioural traits to use this substratum effectively. Silk is used to the best advantage to bind sand, but is also costly. How spiders invest their silk, given that they exist in a low-resource environment, which is unpredictable, deserves further investigation. It serves as a key to their existence in desert sand.

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References


