

Ecology and diet of *Psammoduon deserticola* (Simon) (Araneae: Zodariidae)

R. Rössl* and J. R. Henschel

Desert Ecological Research Unit,
Gobabeb, P. O. Box 1592,
Swakopmund, Namibia

Summary

Psammoduon deserticola (Simon) (Araneae: Zodariidae) is a spider adapted to live in the sandy environments of the Namib Desert. The individuals dive through the sand thus avoiding high temperatures and to find their prey. Several major desert habitats were sampled along transects crossing a dune, inter-dune valley, riverbed and a gravel plain. This indicated that several biotic and abiotic factors influence spider density, namely the occurrence of rain, soft sand, vegetation cover and prey. Food preference and predation were studied in laboratory experiments. The larvae of Tenebrionidae (Coleoptera) proved to be the most important food source for *P. deserticola*, while larvae of Syrphidae (Diptera) were less preferred. Lepidoptera larvae were not preyed on at all, while Thysanura were an occasional supplementary food source. As predators of tenebrionid larvae, *P. deserticola* may play an important role in the food web of the Namib Desert dunes.

Introduction

Sand-dwelling spiders normally occupy burrows that they dig and line with silk, which stabilises the surrounding sand (Lawrence, 1966; Humphreys, 1976; Marshall, 1995; Henschel, 1990, 1998a,b). Several dune spiders do not, however, use silk in this way, but are capable of sand-swimming, or “diving” through unconsolidated sand. Henschel (1998a) described this as one of the characteristics of ultrapsammophily in spiders. Several other animals are also capable of sand-swimming. In the Namib Desert, these include tenebrionid beetles (Coineau *et al.*, 1982), Thysanura (Watson & Irish, 1988), golden moles (Fielden, 1991), and dune lizards (Robinson, 1990). These animals may sand-swim in order to shelter from hostile conditions prevailing on the sand surface or, in the case of predators, in order to forage.

Psammoduon deserticola (Simon, 1910) is a common sand-swimming spider of the Namib Great Sand Sea (Schulze, 1903; Jocqué, 1991), occurring along the entire length and width of this dune field. With its well-developed spines and setae (Jocqué, 1991), this spider is equipped to move through soft sand without digging. Henschel (1998a) found that *P. deserticola* is most numerous on the upper and lower plinths of active dunes and regarded it as one of the few ultrapsammophilous spiders of the Namib.

Does this spider sand-swim merely to escape the great heat and risk of predation on the surface and still forage on the surface as do most other Namib dune spiders (Henschel, 1998a)? Or does it forage within the sand, swimming after its prey? What does this spider feed on and how does it capture its prey?

During the course of a two-year field study on Namib darkling beetle larvae (Coleoptera: Tenebrionidae) (Rössl, in prep.), we captured specimens of *P. deserticola* that occurred in the same microhabitat as the beetle larvae. This enabled us to examine this spider's relationship with the tenebrionid larvae. By keeping the spiders in the laboratory, we were able to observe their swimming, foraging and hunting behaviour, and to establish their prey preferences from feeding experiments using potential prey species that occur in the spider's habitat. This allowed us to form preliminary conclusions concerning the role this spider may play in the dune food web.

Methods

The fieldwork was conducted between January–May 1997 near Gobabeb (Namib-Naukluft Park, Namibia; 23°33'39"S, 15°02'30"E). The average annual rainfall is 21 mm, but 76 mm fell at the DERU weather station at Gobabeb during the study period, resulting in ephemeral grass growth.

A total of ten transects of 100 × 1 m, each divided into 20 equal sections, were laid out in the dunes, interdune valley, riverbed and on the gravel plains. During early morning hours, the ground was excavated to a depth of 10 cm and the soil put into buckets. This was done in order to prevent spiders and other soil-dwelling arthropods escaping into deeper regions. The excavation continued for as long as the sand surface temperature was below 20°C. Thus work on a single transect was finished in about two to five days, according to the surface temperature. Sand from the buckets was sieved with sieves of 1000 µm mesh and the transects were finally restored to their original state. Arthropods were identified and released or used in laboratory experiments.

During the experiments, the spiders were kept in a temperature control room in round vials of 10.5 cm diameter and 12 cm height. A 3 cm bottom layer of moist sand topped by a 6 cm layer of dry sand was used. Summer day conditions of 14L:10D were maintained. The temperature was set at 30°C and the relative humidity at 30%.

Spiders were placed into the vials and were observed for a fortnight. At the beginning and end of each daily experiment, the contents of the vial were sieved through a 710 µm mesh. The spiders were weighed at the beginning and end of the experiments, while their feeding status was recorded daily. Our first experiment had four treatments, each with six replicates. The treatments involved placing one individual of one of the following potential prey species into each vial with a spider: a conspecific spider, a thysanuran (Thysanura: Lepismatidae), a fly larva (Diptera: Syrphidae), a darkling beetle larva (Tenebrionidae: *Namibomodes maculicollis* Koch, or *Eustelopus octoseriatus* Gebien, or *Metropus depressus* (Haag)). In addition, we twice used a moth larva (Lepidoptera: Noctuidae). In a different experiment with 15 replicates each spider was offered one fly larva, a tenebrionid larva, a moth larva, and a

*Present address: Am Silberberg 23, D-01454 Radeberg, Germany.

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thysanuran. All prey that were consumed were replaced until the end of the fortnight. All animals were released at the capture site upon completion of the experiment.

Results

The spiders were found at one location only, namely along one transect in the area under a solitary *Acacia erioloba* tree in an interdune valley 2 km S of Gobabeb. In 35 m² of this area, a total of 174 *P. deserticola* were captured together with 79 tenebrionid larvae, 25 moth larvae and 18 fly larvae, and the numbers of Thysanura and ants were estimated at 18 and 11 respectively. These insects were also found at other places, but the tenebrionid larvae were not as abundant as under the tree. Within an area of 85 m² in the adjacent interdune valley away from the tree only 11 tenebrionid larvae were found.

Our subsequent observations under the tree indicated that spiders remained in the top layer of sand only as long as the temperature was <25°C and moved to deeper layers between 1100–2000h when it was hotter. When released on surfaces at >40°C, the spiders immediately dived deep into the sand, where the temperatures are cooler (Lubin & Henschel, 1990). Spiders died if they were prevented from sand-diving by, for example, stones or compact soil.

The spiders initiate their dive by flipping upside-down and moving downwards into the sand at an angle of about 30°. The front pair of legs point in the direction of movement. The second and third pairs of legs are held transverse to the movement and the fourth pair of legs point backwards, providing thrust. The tips of the front legs appear to move in rapid wriggling movements, which may enable the spider to penetrate the sand layer, while the hind legs seem to push it forwards.

Four attacks on tenebrionid larvae were observed on the sand surface, where the larvae feed. In each case, the spider attacked from behind one flank of the larva. Bites were inflicted either between the head and the first thoracic segment or between the first and second thoracic segments. Prey consumption commenced immediately.

In the single-prey feeding experiment (Table 1), all spiders captured tenebrionid larvae, each spider consuming an average of 2.8 ± 0.9 larvae and gaining $45.6 \pm 25.4\%$ (range 10.1–103.6%) in mass. Only four spiders captured fly larvae, thereby gaining in mass by $16.4 \pm 20.8\%$ (range -3.9–+52.4%). Only one thysanuran was eaten, increasing the predator's mass by

Replicate	Tenebrionid larvae	Fly larvae	Thysanura	Spiders
1	3	2	0	0
2	3	1	0	1
3	4	0	0	1
4	1	1	1	1
5	2	3	0	0
6	4	0	0	0

Table 1: Numbers of prey eaten by *P. deserticola* in single choice experiment. Different spiders used for each treatment.

Spider No.	Tenebrionid larvae	Fly larvae	Thysanura	Lepidoptera larvae
1	3	1	1	0
2	3	1	4	0
3	4	3	2	0
4	3	2	0	0
5	1	1	1	0
6	3	1	0	0
7	1	3	1	0
8	0	1	0	0
9	1	2	0	0
10	2	2	1	0
11	4	4	0	0
12	2	0	2	0
13	2	1	1	0
14	2	2	0	0
15	2	2	2	0

Table 2: Numbers of prey eaten by *P. deserticola* in multiple choice experiment.

2.0%. Three conspecific spiders were consumed, the preying spiders still losing $2.3 \pm 9.9\%$ (range -15.7–+12.5%) in mass. The spiders did not attack either of the Lepidoptera larvae. When given a choice of prey, the spiders each consumed an average of 2.2 ± 0.9 tenebrionid larvae, 1.7 ± 0.8 fly larvae, 1.0 ± 0.8 thysanurans, and no moth larvae (Table 2). Tenebrionid larvae were significantly preferred over fly larvae (Wilcoxon signed rank test=3; $n=15$; $p<0.01$), which were significantly preferred over thysanurans (Wilcoxon signed rank test=1; $n=15$; $p<0.01$). The mass of these spiders increased by $43.6 \pm 32.3\%$ (range -16.1–+99.3%). Spiders that did not feed lost $5.8 \pm 2.6\%$ of their mass. As moisture intake from the sand was possible, this quantity, equivalent to 0.414% mass loss per day, presumably represents metabolic cost.

Discussion

The occurrence of *P. deserticola* in sand under vegetation cover was previously reported by Jocqué (1991), although Henschel (1998a) found this spider also on unshaded dune slopes, and especially on the bare slip-faces. Our record is the highest density ever recorded. This may be the result of good environmental conditions after the unusually heavy rains. Furthermore, the tree-shaded site may represent optimal conditions for both prey and predator. Also, shade may prolong the period of suitable thermal conditions near the surface, extending the foraging hours. Coexistence in high densities may be facilitated by a lack of territoriality and cannibalism.

Psammoduon deserticola captures its prey on the surface. This may make it easier to manoeuvre around the prey for the precision attack, which does not involve the assistance of silk. It is possible, however, that the spiders may also sand-swim in pursuit of prey but this was not observed.

The characteristic method of capturing tenebrionid larvae as well as the spider's preference for this prey type in our experiments supports the suggestion that tenebrionid larvae are the major prey. The consumption

prey increased when the spiders were offered a variety of different prey types. The remarkable increase in the consumption of Thysanura in the presence of other prey could perhaps be due to an increase in surface activity of the Thysanura when coexisting in a compartment with other prey. Lepidoptera were ignored, possibly because their silken tunnels protected them. Ants and termites are other potential prey that were not tested.

The metabolic cost calculated for *P. deserticola* in the laboratory is 25% higher than that found by Lubin & Henschel (1996) for the similar-sized eresid *Seothyra henscheli* Dippenaar-Schoeman of the Namib dunes. This could mainly be the difference between sand-swimming compared with daily web repair. *Psammoduon* may compensate by actively pursuing its prey rather than sitting and waiting. The daily consumption data recorded here are in the order of 3% of the spider's mass, thrice that of other Namib spiders (Henschel, 1994; Lubin & Henschel, 1996). However, the laboratory conditions may not have presented normal feeding conditions and may thus not be comparable.

Psammoduon deserticola is potentially a very important predator in the Namib dunes. Next to golden moles, it is the only predator known to concentrate on tenebrionid larvae that may be difficult to capture for others. Although the large *Leucorchestris arenicola* Lawrence (Heteropodidae) dominates the dunefield as far as spiders are concerned (Henschel, 1990, 1998a), it is a predator of tenebrionid imagos and does not compete directly with *P. deserticola*. The ability of *P. deserticola* to sand-swim may enable it to escape from the aggressive, araneophagous *Leucorchestris*. These two spiders may thus play complementary roles as predators of different life stages of the most important detritivores of the Namib dunes.

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