

THE SUB-SAND NESTS OF *YLLENUS ARENARIUS* (ARANEAE, SALTICIDAE): STRUCTURE, FUNCTION AND CONSTRUCTION BEHAVIOR

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ABSTRACT. An unusual silken nest built under the sand surface is described in *Yllenus arenarius*—a jumping spider inhabiting sandy dunes. In this open habitat, characterized by high temperature and humidity gradients as well as a lack of retreats, the nest probably plays a key role in the survival strategy of *Y. arenarius* that is numerically dominant among day-active, dune-dwelling spiders. These salticids built nests a few millimeters under the surface after burrowing in loose sand. Four types of nests of different size, structure and function were built: A) where eggs were laid and early instars developed, B) where spiders molted, C) where they overwintered and, D) the most common, where spiders spent the night. Different age groups produced different numbers of nests per time unit. Juveniles in their first season of life built many more nests than subadult spiders in their second season, which in turn built more nests than adult spiders. Various functions of the silken nests and the high numbers built by juveniles suggest that the structures may play an important role in surviving in the dune.

Keywords: Salticidae, nest, structure, function, behavior

Yllenus arenarius Menge 1868 is a medium-sized jumping spider with an adult body length of about 6 mm. The spiders inhabit bare areas of sandy dunes primarily in central and eastern Europe (Prószyński 1991; Żabka 1997), tending to keep away from dense vegetation. They are numerically dominant among day-active arachnids. Their life span in the field reaches about 700 days. The spiders hatch in spring and die two years later, overwintering twice (as juveniles and as adults). Thus, in the field, two cohorts can be found simultaneously (Bartos 2000).

Much attention has been paid to spider webs (e.g., Shear 1986; Foelix 1996). Studies on various aspects of webs resulted in our knowledge of the web architecture and web-building behavior of numerous spiders (e.g., Zschokke & Vollrath 1995), as well as the physical and chemical properties of certain web elements (e.g., Peters 1987; Tillinghast & Townley 1987). However, surprisingly little is known about the cocoons and nests. They are all also silken products, possessing distinct structures and properties (Hieber 1985; Nentwig & Heimer 1987; Hieber 1992a,b). Nests are crucial for the spiders' development. They provide stable temperature and humidity con-

ditions for eggs as well as for hatching and molting spiders (Nentwig & Heimer 1987). In the stages when spiders cannot defend themselves against predators, nests also provide safe retreats (Foelix 1996).

Relatively more attention has been paid to the nests of jumping spiders, which are both variable and specialized (Jackson 1985; Hallas & Jackson 1986; Jackson 1989). From these and other studies we know that, apart from the typical functions, nests produced by certain jumping spiders also play an important role in species recognition, courtship, and mating (Jackson 1981, 1982a, b, 1983, 1986). Some of the nests have prey-holding abilities and may play a role in prey capture (Hallas & Jackson 1986). In this paper, the structure, function and building behavior as well as the age-dependent differences in nest building by *Y. arenarius* will be considered.

METHODS

Data were taken in the field as well as in the laboratory. Adult and juvenile individuals of *Yllenus arenarius* were collected from 14 sites in central and eastern Poland. From one of the sites (Kwilno) in central Poland they were collected regularly—every two weeks.

Four measurements were taken of live specimens with a stereomicroscope (precision, 0.1 mm): body length (BL), abdomen length (AL), abdomen width (AW) and posterior eye width (PEW). The sex and age of the spiders were also recorded.

Spiders were kept individually in glass containers (1 liter) with a 3 centimeter-thick layer of dune sand on the bottom. Temperature was ca. 25 °C, light regime 12L: 12D, and the sand was moistened weekly with 5 ml of water. Spiders were fed *ad libitum* (10 fruit flies twice a week). Under these conditions 90 spiders were reared and their nests were collected.

Sand from lab containers was sieved every two weeks in order to collect nests. Nest length (NL) as well as nest width (NW) were measured (precision, 0.1 mm). The measurements were taken from adults or, in the cases of nests used for molting, from subadult spiders. To describe the ratio of nest length (NL) to spider body length (BL), NL/BL was calculated. The ratio of nest width (NW) to spider abdomen width (AW), was given as NW/AW. The nests were opened and checked for eggs and exuvia and to assess nest wall transparency. The wall transparency was assigned to one of three categories according to Jackson (1979): 1—transparent silk; 2—nearly opaque; 3—completely opaque (sand grains were invisible through the silk).

In winter a two centimeter thick layer of sand was collected from the dune surface. Sand was dried in the lab (temperature ca. 25 °C). Spiders active on the sand surface were collected, measured and reared. Dried sand was sieved in order to collect nests and immersed spiders. Burrowing was recorded with a camera and the nest building behavior was analyzed on the basis of observations taken at certain stages of the process, which was interrupted by blowing the sand off the spider during nest building.

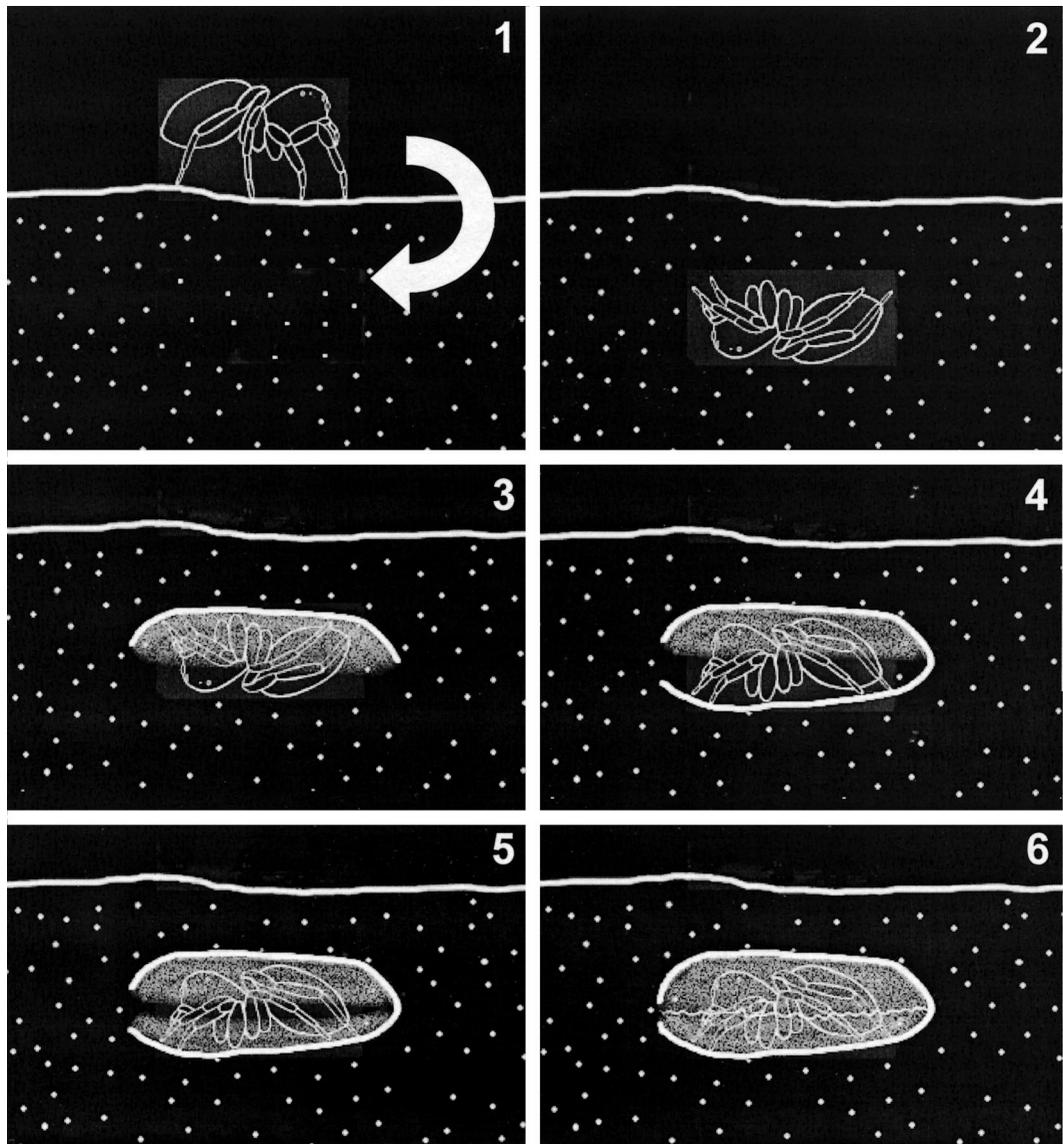
All statistical procedures followed those described by Zar (1984). Comparisons between relative length (NL/BL) and width (NW/AW) of different nest types and the number of nests produced daily were conducted using the Kruskal-Wallis test (H), followed post-hoc by nonparametric Tukey-type multiple comparisons (Q). Data are presented as mean \pm SD (*n*).

RESULTS

Yllenus arenarius was found to build nests under the sand surface (ca. 5 mm under the surface). Before starting to construct a nest spiders dug themselves into the sand (Fig. 1). The spiders immersed themselves in the sand without excavating. They used legs I to scarify and dive into the sand. Legs II were used to push the sand aside, which allowed the spider to pull into the sand. The process of diving took an average of 81.6 ± 43.1 sec. (*n* = 10). A spider immersed in the sand lay upside down and began to build the top wall (the “ceiling”) of the nest (Figs. 2, 3). The sheet of silk was spun and spread aside with the legs. The next stages could not be observed, however the structure of the nest and the spider’s position in the last observed stage suggested that the spider then turned rightside up and spun the bottom wall (the “floor”) of the nest (Figs. 4, 5). Finally both walls were bound together with silk (Fig. 6). This scenario seems reasonable since the nest is made of two thick layers of silk, which are difficult to tear apart. The nest, however, can easily be torn into two pieces along the lateral line, which binds the two walls.

The nest of *Y. arenarius*, as viewed from above, is an oval, pear-shaped or rectangular sac with sand and organic matter glued in the silk. Nests usually had one main opening, which could elastically expand when the spider was leaving the chamber. Sometimes another small aperture was found on the opposite end of the nest. Because of its small diameter (too small for a spider to get through and never used in escape), it was probably an unwoven hole rather than a second opening. Silk inside the nest was probably non-adhesive because sand did not tend to stick to it. The outer layer of silk, however, was adhesive since sand grains stuck to it firmly.

Nests built for various purposes differed in size, structure and wall transparency. The function of different nest types appears obvious when analyzing the nest content, time of the day and season when built. On those bases, the following four nest types were distinguished. Type A (nests where eggs are laid and young spiders develop) were oval or slightly elongated sacs (Table 1). Layers of silk and sand made the walls slightly rigid and convex (wall transparency, 2). The nests con-



Figures 1–6.—Burrowing and nest building in *YlLENUS ARENARIUS*. 1. Spider on the sand surface. 2. Immersed spider in upside down position. 3. Building top wall of nest. 4. Spider after turning rightside up. 5. Building bottom wall of the nest. 6. Binding top and bottom walls together.

tained on average 6 ± 0.8 eggs ($n = 5$). Chorion sheaths and juvenile exuvia were also found there. Two thin, inner walls made of silk were unique for this nest type. One of them covered the eggs so that they were held against the bottom of the nest. The other wall was a vertical one placed close to the entrance separating it from the main chamber containing the eggs. The latter silken layer was made by the female probably after she had laid the

eggs. In the lab, these nests were only found in the spring. Type B (nests where spiders molt) were oval or elongated, convex sacs made of several layers of silk and sand (Table 1) (wall transparency, 2). Exuvia were found only in this type of nest. Type C (nests where spiders overwinter) were densely impregnated with organic matter and the most elongated of all nests—almost tubular (Table 1). The nests were convex and had the thickest walls of all

Table 1 The four nest types of *Y. arenarius* and their measured properties. (NL: nest length, NW: nest width, BL: body length, AW: abdomen width).

Nest type	NL (mm) mean±SD (n)	NW (mm) mean±SD (n)	NL/BL mean±SD (n)	NW/AW mean±SD (n)
A: where eggs and young spiders develop	13.44 ± 1.70 (5)	9.53 ± 1.16 (5)	1.98 ± 0.25 (5)	3.74 ± 0.45 (5)
B: where spiders molt	13.96 ± 3.15 (8)	8.34 ± 1.29 (8)	2.62 ± 0.37 (8)	3.71 ± 1.02 (8)
C: where spiders overwinter	16.12 ± 1.13 (3)	8.89 ± 0.87 (3)	2.42 ± 0.33 (3)	3.21 ± 0.46 (3)
D: where spiders spend the night	8.22 ± 0.74 (6)	6.89 ± 0.52 (5)	1.81 ± 0.74 (32)	3.47 ± 0.58 (32)

types (wall transparency, 3). They were found only in winter sand samples. Type D (nests where spiders spend the night) were round, oval or rectangular with flat walls. They were the most fragile of all nests, with thinnest walls (wall transparency, 1). These nests were produced more often than other types (up to 1 each 24h). Nests collected from the same sample (built by the same individual) varied in size (Table 1). The last nest built (where the spider was found during sieving) was not usually the largest one. Comparison of relative nest length (NL/BL) of all types of nests revealed that type D nests were significantly shorter than type B nests ($Q = 4.54$; $df = 4$; $P < 0.05$) and type C nests ($Q = 2.81$; $df = 4$; $P < 0.05$). The differences in relative nest width (NW/AW) between all types of nests were not significant ($H = 1.21$; $df = 3$; $P > 0.75$).

Spiders in successive age groups built respectively larger nests. Early instars started to build overnight nests soon after leaving the nest, where they hatched (type A). These nests were rectangular and had very thin walls. Nests of later stages were bigger, generally more oval and had thicker walls.

Juvenile spiders in the first and at the beginning of the second year of life built on average 0.94 ± 0.55 nests/day ($n = 129$), which is 18.8 times more than in subadults (0.05 ± 0.12 nests/day, $n = 39$). The difference is significant ($Q = 8.27$; $df = 3$; $P < 0.05$). Juvenile spiders built 31.3 times more nests than adult spiders (0.03 ± 0.06 nests/day; $n = 18$). The difference is also significant ($Q = 6.13$; $df = 3$; $P < 0.05$). The differences between subadult and adult spiders in the number of

nest built daily were not significant ($Q = 0.39$; $df = 3$; $P > 0.05$). Adult spiders were often found immersed in sand but with no nest.

DISCUSSION

Nests built by *Y. arenarius* under the sand surface are an interesting and unique adaptation to survival in dunes. In the sandy habitat characterized by high daily and seasonal temperature and humidity gradients as well as lack of retreats, underground nests provide shelter against night-active predators, strong wind and periods of inclement weather such as heavy rains. Water from rain floods riverside and marine dunes, temporarily inundating the habitat, and may be a severe mortality factor. The waterproof properties of silken walls and their permeability to air, which allows functioning as a physical gill (Hieber 1985, 1992a; Nentwig & Heimer 1987), may significantly reduce the spider's mortality under conditions of flooding. This, however, has not been studied in *Y. arenarius* and requires further research.

Differences in wall transparency (wall thickness) of nests of jumping spiders have already been reported. Jackson (1979) describing variations in the nests of *Phidippus johnsoni* (Peckham & Peckham, 1883) mentioned that nests where molting and oviposition took place were made of dense silk. This study confirmed that observation. The lower wall transparency (the higher wall thickness) in these kinds of nests is probably related to the high susceptibility of eggs and spiders during molting to changes in humidity (Hieber 1992a). The differences in wall thickness re-

sult in its rigidity and may therefore influence the shape of the nest.

Jumping spiders differ as to whether they return to previously built nests. A study by Jackson (1979) of *P. johnsoni* revealed that the spiders employ the same nest for prolonged periods, while lack of homing behavior was found in *Salticus scenicus* (Clerck 1757) (Plett 1962). In case of *Y. arenarius* there are several observations strongly supporting the idea that the spiders do not use their nests repeatedly. Juveniles build a new nest on average every day and later instars were usually found with more than one nest in the lab sand sample. After leaving a nest, a little pit, indicating where the spider emerged onto the surface is very quickly filled with wind blown sand. Nests are built in areas of almost bare sand with very few structures allowing landmark orientation. The wandering spider is unlikely to be able to recognize or localize the nest site when it has emerged from its underground nest. Furthermore, a spider returning to the nest would bring in some grains of sand, which were never found in the nests.

The importance of the nests where spiders molt, lay eggs and overwinter is not in doubt. These functions were never recorded outside the nests. The function of the overnight nests is much less clear. Adult spiders were found spending the night in the sand without the nest, so the nest does not appear to be crucial for their survival. If adult spiders were found to build few overnight nests but juveniles found to build many, one could conclude that the nest plays a more important role for juveniles. It is possible that the difference in the number of nests produced at different ages is related to a higher susceptibility to humidity changes in juvenile spiders especially during molting (Hieber 1992a). In adult spiders the costs connected with silk production and nest building may be higher than the advantages of using a nest. The surface to volume ratio is lower in the case of an adult's nests than in a juvenile's nests (which implies that the latter should use relatively more silk). The silk threads, however, produced by juveniles are thinner and the layers of silk building the nest walls may be fewer, suggested by the higher rate of damaged nests.

This study is the first attempt to describe and understand the variability of nests and unusual nest building behavior in *Y. arenarius*.

Further studies to determine nest function are clearly needed.

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