INSTABILITY OF SANDY SOIL ON THE LAKE WALES RIDGE AFFECTS BURROWING BY WOLF SPIDERS (ARANEAE: LYCOSIDAE) AND ANTLIONS (NEUROPTERA: MYRMELEONTIDAE)

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ABSTRACT

Tests with *Geolycosa* spiders revealed that these arachnids may be excluded largely from the Ridge Sandhill-turkey oak ecosystem on the Lake Wales Ridge because their burrows quickly collapse in the unstable natural soil (Astatula sand). Comparable results were obtained in tests of pit construction by antlion larvae (Myrmeleontidae), which may serve as bioindicators of soil stability.

Key Words: *Geolycosa*, *Myrmeleon*, Florida scrub, sandhill, ecology, behavior

RESUMEN

Pruebas con la araña *Geolycosa* demuestran que esta especie puede ser excluídas del ecosistema de "Southern Ridge Sandhill-turkey oak" en la loma de Lake Wales, dado que sus madrigueras se derrumban rápidamente en el suelo natural inestable (arena "Astatula"). Resultados semejantes fueron obtenidos en pruebas de hoyos excavados por larvas de la hormiga león (Myrmeleontidae), lo cual podría ser utilizado como un bio-indicador de la estabilidad del suelo.

The scrub and sandhill ecosystems on the Lake Wales Ridge in central Florida are major centers of endemism that now harbor many rare and endangered species (Deyrup & Eisner 1993, 1996, Dobson et al. 1997, Ando et al. 1998). These xeric, upland communities consist of a complex patchwork of approximately 15 distinct vegetative associations, most of which depend on periodic fire to maintain species diversity (Abrahamson et al. 1984).

Quantitative field studies conducted annually from 1993-1999 at Archbold Biological Station, located at the southern terminus of the Lake Wales Ridge, reveal that two burrowing wolf spiders endemic to Florida scrub, *Geolycosa xera archboldi* and *G. hubbelli*, are numerous in all but one vegetative association, namely Ridge Sandhill with turkey oak (RSt) (J. Carrel, unpublished results). This observation is quite surprising because other wolf spiders (genus *Lycosa*) are plentiful in the RSt habitat and *Geolycosa* themselves are numerous in all neighboring habitats, such as Hickory Scrub (RSh) and Scrubby Flatwoods (SF) (See Richman et al. 1995 for a list of local wolf spiders). In addition, because all of the study sites had been burned several years before our studies as part of the station's fire management plan (Main & Menges 1997), there were many patches of barren sand suitable for *Geolycosa* to colonize (Carrel 1995, Marshall 1995a, Marshall et al. 1999).

We reasoned that the excessive instability of dry soil present in the RSt habitat might make it unsuitable for *Geolycosa* either to construct or to maintain their simple burrows. The burrows are open tubes, 2-15 mm in diameter, lined with silk only at the top, which extend vertically down 4-15 cm, ending in a bulbous chamber (McCrone 1963, Wallace 1942, Corey 1991, J. Carrel, unpublished data). Moreover, we hypothesized that antlion larvae (*Myrmeleon crudelis* Walker) might be particularly useful as bioindicators of soil instability because it is known that these insects will actively seek out fine grained, stable sands for pit construction and that their pits made in fine grain sand are less symmetrical than those made in coarse grained sands (Lucas 1982, 1986, 1989). To evaluate our ideas, we analyzed published survey data for soils found in the RSt and SF habitats, we determined persistence of artificial spider burrows constructed in both habitats, and we studied burrowing by spiders and antlion larvae in the different soils.

Materials and Methods

Soil and Weather Data

We conducted our tests during the dry season (February) at the Archbold Biological Station, Highlands County, Florida. We analyzed data on the Astatula soil in the RSt ecosystem and, for comparison, on Satellite soil in the SF ecosystem published by Carter et al. (1989) in a recent soil survey of Highlands Country. They used the Archbold Biological Station as a primary reference site for these sandy upland soils because the managed ecosystems at the Station, for the most part, represent presettlement conditions on the Lake Wales Ridge. We obtained weather information daily during our tests from the local weather center, which has been in operation at the Station since 1932.

Tests Using Artificial *Geolycosa* Burrows

This experiment was designed to test whether artificial *Geolycosa* burrows constructed in Astatula soil within the RSt habitat would persist as long as those constructed in Satellite soil within the SF habitat.

On 5-II-1996, one day after a heavy (2.9 cm) rain had soaked the soil, we set up 10 stations at 10 m intervals along a transect on each soil type. We chose localities that had been burned two or three times in the past two decades as part of a management plan designed to simulate presettlement burning patterns. At each station we extracted 14 cores, 7 mm diameter by 150 mm deep, in the sand using a piece of tubular steel taken from a television antenna, for a total of 140 cores/soil type. The cores were comparable in size to natural *Geolycosa* burrows. Subsequently on day 1, 2, 4, 6, 8, 10, or 12 thereafter we randomly selected one hole at each station and plumbed its depth to the nearest mm with a narrow rod. During this test there was no precipitation except on day 11 (1.3 cm rainfall) and air temperatures were relatively cool (average ~13°C, range: -6° to 27°C).

Tests Using Living *Geolycosa*

These tests were designed to determine two things: (1) whether the burrows constructed by *Geolycosa* spiders in Astatula soil from the RSt ecosystem are comparable to those they make in Satellite soil from the SF ecosystem, and (2) whether, after removal of the resident spiders, unoccupied burrows in Astatula soil would persist as long as unoccupied burrows of comparable size made in Satellite soil.

We reconstructed natural profiles of Astatula and Satellite soils to a depth of 12 cm in plastic flower pots (15 cm diameter × 15 cm height, N = 10 for each soil type) by excavating three layers (0-2, 2-8, and 8-12 cm depth) of each soil separately and then adding them in reverse order to the pots after passing each through a coarse (4 mm mesh size) sieve to remove roots and debris. On 13-II-1995, the pots were partially buried with sand in an open firelane near the weather station after they were arranged in five columns of four pots each using a complete random block design. To each pot we added one adult or subadult *Geolycosa hubbelli* chosen at random from 20 spiders we had recently dug out of their burrows in Satellite sand and weighed to the nearest mg. We also placed four or five dried leaves on the sand for each spider to use to build the turrets that they characteristically construct around their burrow entrances. Each pot was tightly covered with a piece of nylon mesh fabric to retain the spider and then entire assemblage of 20 pots was covered with a sheet of coarse hardware cloth attached to a heavy wooden frame to prevent disturbance by raccoons and other mammals.

We measured the depth of each spider burrow to the nearest mm at 2 days and again at 10 days by plumbing it gently with a thin rod. Subsequently all spiders were removed without damaging the burrows after we lured them out of their burrows with a mealworm (the larva of the beetle *Tenebrio molitor*) tethered to a piece of thread. The diameter of each burrow was measured to the nearest 0.1 mm with calipers. Following this, the pots were covered again with the nylon fabric and hardware cloth and left *in situ* for 4 days before the depths of the unoccupied burrows were measured as before.

On the first day of this experiment, shortly after the spiders were set up, there was light rain (0.5 cm), followed by heavy rain (3.1 cm) on the next day. Thereafter it did not rain until day 8 when a total of 2.8 cm precipitation fell. During these tests daily air temperatures were relatively warm (average ~20°C, range: 3° to 32°C).

Tests Using Antlion Larvae

Antlion larvae (*Myrmeleon crudelis*, N ~ 50) were collected individually in vials on 28-II-1998, from sheltered areas beside buildings at the Station, as was done previously by Lucas (1986, 1989b), and brought into the laboratory (24-27°C, 16L: 8 D). After inspecting the head capsule for key characteristics (Lucas & Stange 1981), we arranged them in order by body size and then chose 40 medium sized, second and third instar larvae, returning the largest and smallest individuals to the field. We randomly assigned the remaining larvae singly to plastic pots (11 cm diameter × 11 cm height) filled to 10 cm depth either with Astatula soil from the RSt ecosystem or with Satellite soil from the SF ecosystem. The soil originally was scraped from the uppermost 10 cm in the field and air dried at room temperature for one week before sieving to remove roots and debris.

At 24 and 48 hr we checked each pot for the presence or absence of an antlion pit and relocation of a pit in the otherwise level sand. We classified an antlion larva as having relocated by the presence of trails in the sand or the presence of a shallow depression where the old pit had been located. After 48 hr we measured the diameter of each pit on its two major axes, corresponding to the anterior-posterior and left-right position of the antlion resting at the bottom of the pit, and the maximum depth of the pit to the nearest mm using calipers (Lucas 1989b). To assess the asymmetry of each pit, we calculated the arithmetic difference between the two diametric measurements.

Representative specimens of *G. hubbelli* and *M. crudelis* were preserved in the collection of arthropods at the Archbold Biological Station.

Results

Interpretation of Soil Survey Data

By overlaying the vegetation map of Abrahamson et al. (1984) with the general soil map of Carter et al. (1989), we determined that the Ridge Sandhill with turkey oak (RSt) ecosystem at the Archbold Biological Station is located predominantly on Astatula soil and the Scrubby Flatwoods (SF) ecosystem is extensively found on Satellite soil. As are all other soils of the upland ridges in Highlands County, both Astatula and Satellite soils are nearly level or gently sloping and they are sandy to a depth greater than 2 m. Astatula soil, prized for citrus production, is excessively well drained; in contrast, Satellite soil is somewhat poorly drained (Carter et al. 1989).

The size distribution of soil particles in the upper 20 cm of Astatula soil is very different from Satellite and most other soils on the Lake Wales Ridge, otherwise these soils all have remarkably similar properties. As shown in Table 1, Astatula soil is a mixture of mostly medium and coarse sand. In contrast, Satellite soil has little coarse sand, but much medium and fine sand. Biophysical calculations demonstrate that larger sand particles are more likely to fall down a slope than smaller ones under dry conditions (Lucas 1982), so the soil survey data led us to predict that burrows of spiders and antlions in coarse Astatula soil would be inherently less stable than comparable burrows made in fine Satellite soil. In addition, the small amount of clay present only in Astatula soil might account for the slight crustiness of surficial material we commonly detect in the RSt ecosystem that is absent from the SF ecosystem. Results of tests reported here confirm our predictions.

Tests Using Artificial *Geolycosa* Burrows

Cylindrical holes in Astatula soil, constructed by us to simulate open *Geolycosa* burrows, filled up with soil particles faster than those made in Satellite soil (Fig. 1). The slope of the regression line decreased from 9.86 mm sand accumulated/d in the Astatula soil to 5.45 mm sand accumulated/d in the Satellite soil. After 12 days the holes in Astatula sand were significantly shallower than those in Satellite sand (Mann-Whitney U-test or Student's t-test, $P < 0.05$). In fact, on day 12 the openings for six of ten artificial burrows in the Astatula sand were barely detectable, whereas only two of ten holes in Satellite sand were hard for us to see.

TABLE 1. PHYSICAL PROPERTIES OF TWO SOIL TYPES USED IN THIS STUDY*.

		Particle size distribution (%)				
Habitat type	Soil series	Coarse & medium sand	Fine & very fine sand	Silt	Clay	Drainage
Ridge sandhill with turkey oak (RSt)	Astatula	81.0	17.3	0.3	1.4	Excessive
Scrubby flatwoods (SF)	Satellite	46.1	51.9	1.5	0.5	Somewhat poor

*Data from L. J. Carter et al. (1989).

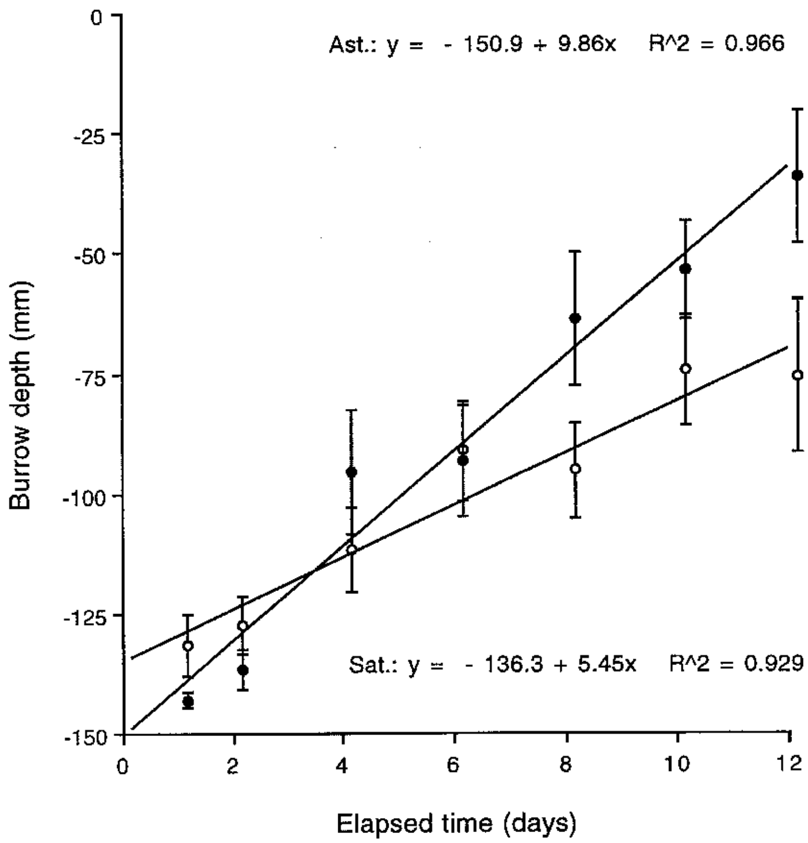

Fig. 1. Artificial *Geolycosa* spider burrows dug in Astatula soil (Ast., solid circles) refill faster than those dug to the same depth in Satellite soil (Sat., open circles). Means, standard errors, and best fit regression equations are indicated.

Tests Using Living *Geolycosa*

Geolycosa spiders burrowed equally well in both soils (Table 2). Within two days each spider had constructed a complete burrow, as indicated by the fact that in the subsequent 8 days they did not significantly deepen their burrows even though there was sand remaining beneath them (Mann Whitney U-test or Student's t-test, $P > 0.05$). In addition, the burrow entrances in each soil type were equivalent in diameter (11.4 ± 0.8 mm for Astatula soil; 12.3 ± 0.4 mm for Satellite soil; Mann-Whitney U-test or Student's t-test, $P > 0.1$).

However, after removal of the wolf spiders, unoccupied burrows in Astatula soil collapsed and filled in more extensively than those in Satellite soil (Table 2). This happened despite the fact that there were no rain storms or strong gusts of wind during the four day interval and the firmly seated pots had a protective cover of netting and

TABLE 2. BURROW CONSTRUCTION BY *GEOLYCOSA* SPIDERS AND PERSISTENCE OF UNOCCUPIED SPIDER BURROWS IN TWO SOIL TYPES.

Elapsed time (days)	Burrow depth (mm, $\bar{X}$ ± SEM, N = 10)		
	Astatula soil	Satellite soil	*P* value*
2	89 ± 6	85 ± 8	n.s.
10	88 ± 7	93 ± 5	n.s.
Spiders removed			
14	48 ± 9	71 ± 7	<0.05

*Pairwise comparison by soil type in each row, Mann-Whitney U-test or Student's t-test, n.s. = not significant.

hardware cloth. At the end of the experiment (day 14) we did not notice any difference in the entrances of the spider burrows or the surrounding sand in the pots, so sand that accumulated within spider burrows had to be of subterranean origin.

Tests Using Antlion Larvae

The pits constructed by antlion larvae (*M. crudelis*) ranged from 20-40 mm in diameter and 8-27 mm in depth, but overall there was no significant difference in size between those made in Astatula and Satellite soils. However, we found that *M. crudelis* pits made in Astatula soil were more symmetrical than those made in Satellite soil (Mann-Whitney U-test, U = 287.5, $P < 0.02$). Knowing that asymmetrical pits are a design feature for improved prey capture whose implementation is impeded by large grains of sand (Lucas 1982, 1989), our results indicate that Astatula soil was less suitable than Satellite soil for pit construction by antlion larvae.

We also found each day that twice as many antlions (6-8 larvae) in the coarse Astatula soil relocated their pits than those (3-4 larvae) in the relatively fine-grained Satellite soil. The daily differences for each pit relocation by soil type were significant ($\chi^2 = 7.75$, $P < 0.01$, df = 1 for day 1; $\chi^2 = 5.05$, $P < 0.05$, df = 1 for day 2).

DISCUSSION

The absence of *Geolycosa* spiders from the Ridge Sandhill with turkey oak (RSt) ecosystem at the Archbold Biological Station cannot be explained primarily by a lack of colonizing spiders. *Geolycosa* spiders are abundant in the Hickory Scrub (RSh) and the Scrubby Flatwoods (SF) that adjoin the somewhat more elevated RSt ecosystem (J. Carrel, unpublished observations), so the source population is large. Although *Geolycosa* endemic to scrub may exhibit limited dispersal (~0.4 m/day) (Marshall 1995b), given many months they can easily cover the 50-100 m distance needed to invade the RSt ecosystem. In fact, in 1997 and 1998 we detected several *Geolycosa* burrows located in the RSt, but never actually in the native vegetation: the spiders always were restricted to footpaths where mats of centipede grass (*Eremochloa ophiuroides*) and wire grass (*Aristida stricta*) reinforced the soil. *Geolycosa* are known to invade and propagate extensively in SF ecosystems at the Archbold Biological Station within one year after a burn rids the soil of leaf litter and many barren patches are created (Carrel 1995).

Our tests indicate that *Geolycosa* spiders and antlion larvae can successfully build burrows in the Astatula soil found in the RSt ecosystem, but soon thereafter the burrows and pits begin to collapse. This suggests the long-term outlook for these arthropods in the RSt ecosystem may be bleak: they must persistently work and expend considerable energy to maintain their subterranean homes or risk burial by subsiding sand. In addition, based on ecological studies of antlion larvae by Youthed & Moran (1969) and Gotelli (1993), we suspect the temperature and moisture regimes in Astatula soil on the Lake Wales Ridge may prove stressful to burrowing spiders and antlion larvae.

One cannot help but wonder if soil instability drives the *Geolycosa* spiders and antlion larvae to abandon their burrows in the RSt ecosystem. Both species of *Geolycosa* living in their preferred habitats (i.e., different types of scrub) at the Archbold Biological Station are known to relocate their burrows at a low frequency (~1-3% per day) (Marshall 1995a, J Carrel, unpublished results). Likewise, antlion larvae relocate their pits very infrequently unless they are disturbed (Heinrich & Heinrich 1984, Matsura 1987). Perhaps after colonizing the RSt ecosystem these arthropods abandon their burrows at such a high rate that there is a tendency for local populations to decline or, in some instances, to go extinct. In particular, the act of relocating burrows and actively maintaining existing ones probably puts the occupants at heightened risk from attacks by enemies, such as birds, pompilid wasps, and spiders, including cannibalistic *Geolycosa* (Marshall 1995b). To our knowledge, there are no published reports on the affect of soil type on the distribution and survival of either *Geolycosa* spiders or antlion larvae. Currently we are conducting field tests to determine rates of site abandonment and survivorship of *Geolycosa* and antlion larvae introduced into RSt and SF ecosystems at the Archbold Biological Station.

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