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THE INFLUENCE OF MOUND STRUCTURE ON THE DIVERSITY OF SPIDERS (ARANEAE) INHABITING THE ABANDONED MOUNDS OF THE SNOUTED HARVESTER TERMITE *TRINERVITERMES TRINERVOIDES*

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ABSTRACT. The dynamics of spiders present in abandoned *Trinervitermes trinervoides* (Sjöstedt) termite mounds were studied over a period of one year, from March 1999 to January 2000, with five mounds excavated on a bimonthly basis. All spiders present in the mound were collected by hand and preserved in 70% ethanol. A total of 771 spiders represented by 21 families and 82 species were collected from the 30 mounds during the course of the study. The most abundant were the Gnaphosidae, which represented 37.87% of all spiders collected, followed by the Salticidae (12.97%), Pholcidae (10.51%) and Oonopidae (9.60%). These were the only families that represented more than 5% of the spider fauna. The most abundant species were *Zelotes fuligineus* (Purcell 1907) (Gnaphosidae) (11.69%), *Smeringopus sambesicus* Kraus 1957 (Pholcidae) (10.51%), *Heliophanus* sp. (Salticidae) (9,86%) and a Gamasomorphinae sp. (Oonopidae) (9.21%). A correlation was found between spider abundance and mound height, surface perforation of the mound and season of collection. Spider numbers were highest in mounds with a high surface degradation, while a tendency existed for an increase in numbers with increased mound height. Web-building spiders (Pholcidae and Theridiidae) were largely limited to mounds with a cavity in the structure.

Keywords: Termite mounds, spiders, mound structure

Knowledge of the spiders in southern Africa is largely limited to species descriptions, while their ecology remains relatively unexplored. However, during the last two decades there has been an increase in research into the diversity and ecology of spiders in southern Africa. Research on spiders in natural habitats has addressed diversity in grassland (Lotz, Seaman & Kok 1991), savanna (Dippenaar-Schoeman, van den Berg & van den Berg 1989), Nama Karoo Biome (Dippenaar-Schoeman, Leroy, de Jager & van den Berg 1999), the fynbos biome (Coetzee, Dippenaar-Schoeman & van den Berg 1990), pine plantations (van den Berg & Dippenaar-Schoeman 1988), and indigenous forests and pine plantations (van der Merwe, Dippenaar-Schoeman & Scholtz 1996).

The research on the association of spiders with termites in southern Africa has thus far only involved two widespread termite species, namely the harvester termite *Hodotermes mossambicus* (Hagen), dealt with by Dippenaar & Meyer (1980), van den Berg & Dippenaar-Schoeman (1991), Jocqué & Dippenaar-Schoeman (1992), and Dippenaar-Schoeman, de Jager & van den Berg (1996 a,b), and the fungus growing termite *Odontotermes transvaalensis* (Sjöstedt), investigated by Cumming (1993) and Wesolowska & Cumming (1999).

Until now the spiders associated with the mound-building snouted harvester termite *Trinervitermes trinervoides* (Sjöstedt) have not been investigated. This termite species is particularly abundant in the grassland and savanna regions of central South Africa, and constructs dome-shaped mounds (Meyer 1997). The death of a queen and subsequent deficiency of a successor has the effect of the colony declining in number as no more progeny is produced to replace termites that die or are preyed upon (R. Adam, pers. comm.). The queen's death never has the consequence of immediate mass mortality of the colony, but in most cases ''abandoned'' mounds do contain termites, mainly workers, which are remnants of the colony that previously occupied the mound. Ultimately the mound will become a dead structure with no termites. Abandoned *T. trinervoides* termite mounds form an important part of the grassland ecosystem in the Free State, serving as a refuge for a wide variety of vertebrates (reptiles and mammals) and invertebrates (spiders, scorpions, mites and insects). The mounds are slowly degraded by weathering and the digging of termitivorous mammals such as *Orycteropus afer* (aardvark), exposing the mound surface to colonization by such opportunistic organisms.

The interaction between the spiders and the termites varies and three possible interactions exist: termitophilous species, which reside permanently in the termite mound; spiders that live in close association with the termites and prey on them, also known as termitophages; and spiders that use mounds as a shelter and for occasional food. The latter case will be dealt with here. This is the second study on spiders of grassland in the Free State, South Africa and the first of three papers reporting on spider diversity associated with the abandoned mounds of *T. trinervoides*. This study forms part of the South African National Survey of Arachnida (SANSA).

METHODS

Study area and period.—The farm Deelhoek is situated approximately 38 km northwest of Bloemfontein (28° 54′ S, 26° 07′ E) in the Free State at an elevation of approximately 1250 m. The farm comprises 350 ha of cultivated lands and 768 ha of grassland dominated by *Themeda triandra*, *Cymbopogon* and *Eragrostis* grasses. The farm falls within the summer rainfall region of South Africa, with the annual rainfall averaging 400–500 mm. The mounds studied were located in the grassland section of the farm, which contained a red soil substrate with a partially rocky composition in the northern and eastern parts. The spiders in the abandoned termite mounds were studied over a period of 11 months from March 1999 to January 2000, with five mounds excavated on a bimonthly basis to search and locate all spiders sheltered within.

Mound parameters.—A brief description of the mound (height and degree of perforation of the exterior surface), the condition of the surrounding grassland, as well as the weather conditions was made prior to the excavations.

Degree of perforation (DOP) describes the degree of disintegration of the outer surface of the mound either by weather conditions such as wind and rain, or by digging actions of aardvark or other termitophagous mammals. Such weathering would typically be repaired if an active colony was residing in a mound, but once the queen has died, no repairs are done and the structure gradually breaks down. A value was assigned to each mound depending on the proportion of the surface with exposed tunnels. A higher percentage value indicates a more advanced stage of disintegration. A DOP of 100% indicates a mound with a minimal number of tunnels remaining exposed to the outside and the majority of the exterior surface disintegrated and sandy. A DOP of 90% shows that the exterior of the mound has started to break up or disintegrate. A DOP of 80% indicates that the entire surface of the mound is weathered and the tunnels in the mound are all exposed to the environment outside the mound. As this represents the entire surface of the mound (8/8), mounds with a DOP of 70% and less have a relative proportion (in eighths) of the surface weathered with exposed tunnels. For example, mounds with 60% DOP have 6/8 of the surface with exposed tunnels, etc.

The height of the mound was measured with a meter rule. Mound height is important in determining the amount of living space available to the mound inhabitants. The presence or absence of cavities in the mound structure further affects the volume of living space and distribution of organisms due to niche variation, while at the same time providing a microhabitat for occupation by sedentary web-building spiders. Cavities are typically hollow spaces within the mound structure or on the outside of the mound where mammals have dug, and are usually greater than 0.5 dm^3 in volume. In comparison, tunnels are at the very most 12 mm in diameter.

Collecting methods.—Five mounds were dug open in their entirety during each of the six sampling periods using a pitchfork. Mounds were randomly selected, but emphasis was placed on trying to excavate mounds of different heights and DOP. Excavation began with the dome of the mound and proceeded to the tunnels beneath the ground level. Sections of the mound were broken into smaller pieces so that the tunnels could be examined to collect all spiders with an aspirator or jar in 70% ethanol. Notes were also made on the non-aranean fauna inside the mound, with special reference to the quantity of termites remaining in the mounds. Following excavation an estimate of the remaining termite population was made (calculated as a percentage of an active colony in a mound of the same size). If any cavities were present in the mound structure an estimate of their volume (in dm^3) was made.

Due to taxonomic problems within some families and the high number of immatures collected, numerous specimens could only be identified to generic, or in a few cases, to family or subfamily level. Voucher specimens have been deposited in the National Collection of Arachnida at ARC- Plant Protection Research Institute in Pretoria, South Africa.

RESULTS AND DISCUSSION

Numbers and species present.—A total of 771 individuals were collected from the 30 mounds representing 21 families and 82 species (Table 1). The most abundant family was the Gnaphosidae representing 37.87% of the total number of spiders, followed by the Salticidae (12.97%), Pholcidae (10.51%) and Oonopidae (9.60%). These were the only families that represented more than 5% of the spider fauna.

The most abundant species were *Zelotes fuligineus* (Purcell 1907) (Gnaphosidae, 11.69%), *Smeringopus sambesicus* Kraus 1957 (Pholcidae, 10.51%), *Heliophanus* sp. (Salticidae, 9.86%) and a Gamasomorphinae sp. (Oonopidae, 9.21%). These were the only species constituting more than 5% of the total. Twenty-one of the 82 species (25.6%) were represented by single individuals. A greater diversity of spiders was collected in this study compared to a study on spiders associated with the harvester termite *Hodotermes mossambicus*, in which 55 species were collected (van den Berg & Dippenaar-Schoeman 1991).

Table 1. Family composition of spiders collected from *Trinervitermes trinervoides* mounds on the farm Deelhoek, Bloemfontein, showing abundance and species diversity from thirty mounds sampled.

Family	Total collected	% of Total	Total species	% of Total
Ammoxenidae	5	0.65	1	1.22
Agelenidae	2	0.26	1	1.22
Caponiidae	18	2.34	1	1.22
Corinnidae	10	1.30	4	4.88
Ctenizidae	3	0.39	1	1.22
Dictynidae	1	0.13	1	1.22
Eresidae	5	0.65	1	1.22
Gnaphosidae	292	37.87	29	35.37
Hahniidae	1	0.13	1	1.22
Linyphiidae	21	2.72	2	2.44
Liocranidae	32	4.15	5	6.10
Lycosidae	10	1.30	5	6.10
Mimetidae	3	0.39	1	1.22
Oonopidae	74	9.60	2	2.44
Palpimanidae	5	0.65	3	3.66
Philodromidae	4	0.52	2	2.44
Pholcidae	81	10.51	1	1.22
Prodidomidae	38	4.93	6	7.32
Salticidae	100	12.97	7	8.54
Theridiidae	34	4.41	6	7.32
Zodariidae	32	4.15	2	1.22
Σ	771		82	

Van den Berg & Dippenaar-Schoeman (1991) found that gnaphosids represented 20.0% of the species in an area where *H. mossambicus* was found. In this study the gnaphosids were also the most diverse family, accounting for 35.37% of the species collected (Table 1). This indicates that gnaphosids often represent the most diverse and abundant group of spiders in the grassland biome in southern Africa (see also Lotz et al. 1991).

Spiders in web building families are more likely to remain in the mounds for a longer period of time following construction of their webs, e.g. *S. sambesicus*. Communal webs of this species were observed in single termitaria for as long as 6 weeks.

Ground wanderers, which were more abundant, are for the most part active hunters and the more common species may forage within the mound and its surroundings. Rare species may accidentally wander in and out of the mound, or use it as an overwintering facility. The salticid *Heliophanus* sp. and Gamaso-

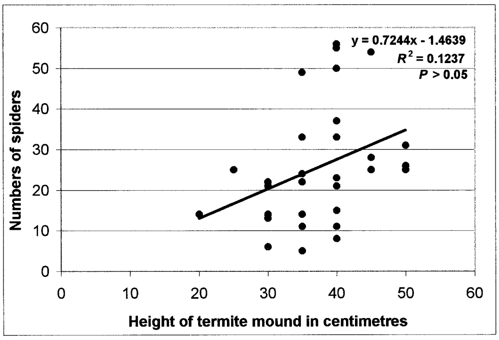

Figure 1.—Linear regression of total spider numbers versus the estimated height (in centimeters) of abandoned mounds of the termite *Trinervitermes trinervoides*, sampled between March 1999 and January 2000 at Deelhoek, Bloemfontein.

morphinae sp. (Oonopidae) appear to be the only species collected that are specifically associated with these abandoned mounds, as they were neither collected on grass or in pitfalls in the surrounding grassland. These two were of the most abundant species collected, and also represent the bulk of the individuals collected from each family, i.e. 76.0% and 97.3%, respectively. Nothing is presently known about the means by which the mounds are located by these spiders.

Influence of mound height on abundance.—The spider abundance in the 30 mounds sampled was plotted against the mound height measured prior to sampling, and a linear trendline extrapolated (Fig. 1). Despite the uneven distribution of the mound heights, the majority being between 30 and 40 cm high, the linear progression shows that with an increase in mound height there is an increase in spider abundance. This is to be expected as the mounds of *T. trinervoides* take the shape of a dome (Meyer 1997), and consequently the slightest difference in height has a fairly significant influence on the surface area and volume of the mound. However, the highly variable numbers of spiders encountered within a given height range make it difficult to accurately predict the spider abundance for a specific height. Although expected to be a major influence on spider abundance, this relationship was found to be not significant ($R^2 = 0.1237$, $P > 0.05$). The maze-like interior of the mound may make it difficult for spiders to find their way out once they have entered the mounds, especially in the case of ground wanderers such as gnaphosids that are not specially adapted the mound habitat. The exception may be the two likely specialists mentioned above, which have probably adapted to negotiate their way around the mounds successfully.

Influence of degree of perforation.—The mean numbers of spiders per mound were highest in mounds with a DOP of 60–80% (Table 2), with numbers considerably lower when the surface was severely degraded (DOP's of 90–100%). A combination of a substrate of loose sand (which may not be as suitable as a firm surface for ground wandering spiders with running-hunting lifestyles that have to search for their prey) and a low number of exit holes may result in spiders not even entering such mounds. Numbers were also low when the number of entrance holes were minimal (≤ 50%). The high number of exposed tunnels and hard surface at DOP's of 60–80% is probably responsible for the highest spider abundance in these mounds.

To determine the effect that degree of perforation (DOP) had on spider abundance it was necessary to consider the effect of mound

Table 2. Analysis of the relationship between mound height and spider abundance for six categories of degree of perforation (DOP) of abandoned *Trinervitermes trinervoides* mounds at Deelhoek, Bloemfontein.

Degree of perforation	50%	60%	70%	80%	90%	100%
Number of mounds	4	5	5	6	5	5
Mean mound height	41.25	42.00	37.00	36.67	36.00	33.00
Number of spiders	72	175	156	170	83	105
Mean spiders per mound	18.00	35.00	31.20	28.33	16.60	21.00
Standard deviation	8.52	19.25	13.07	20.95	9.71	5.70
Ratio of mean spiders: mean mound height	0.44	0.83	0.84	0.77	0.46	0.64

height as well. By calculating the relationship between mean mound height and spider abundance for each of the six categories of DOP sampled, a similar pattern emerged: numbers of spiders are highest at DOP's of 60–80%, irrespective of the height of the mounds (Table 2).

Cavities in the mound structure.—Web-building spiders (e.g. Pholcidae and Theridiidae) were largely limited to mounds with a cavity in the structure. Most web-building families (e.g. Agelenidae, Dictynidae, Eresidae, Hahniidae and Linyphiidae) were found in tunnels inside the mounds, while pholcids and theridiids were found in cavities in the center or on the outside of the mound structure. Numbers of *S. sambesicus* showed no relationship to season but may be affected by the life cycle of the species. The highest number of *S. sambesicus* collected from a single mound was 38 specimens, 31 of which were immatures. It appears that if the cavity is large enough immatures will remain in a particular mound and co-exist on a social basis, sharing a common web and possibly feeding together on prey caught in the web. It is presently not known whether some of the spiders will leave a particular mound as they approach adulthood, not only due to increased intraspecific competition for food and spatial resources, but also for reproductive purposes.

Heidger (1988) found that *Smeringopus pallidus* (Blackwall 1858) co-inhabits abandoned mammal burrows together with two other web building spiders, *Olorunia ocellata* Pocock 1900 (Agelenidae) and *Euprosthenops proximus* Lessert 1916 (Pisauridae), and may display kleptoparasitic behavior in view of the weak criss-cross threads that it constructs above the webs of the two other species. The webs of *S. pallidus* are too weak to catch large insect prey. In the case of *S. sambesicus* inhabiting abandoned *T. trinervoides* termitaria, however, the webs were relatively dense, and as no other web builders were present, this species is able to catch its own prey and does not rely on a kleptoparasitic lifestyle for survival.

The numbers of *S. sambesicus* were highest in mounds in which the cavity was located on the outside of the mound or was linked to the outside by a space, as opposed to a hollow in the center of the mound structure. A pholcid would struggle to navigate its way along the narrow tunnels to a cavity inside the mound.

Presence of termites.—High *T. trinervoides* densities (maximum of 40%) in abandoned mounds seemed to negatively affect the densities of spiders, probably due to the repellent chemicals produced by soldier termites. Spider numbers were generally highest at low densities of *T. trinervoides*. This was especially prevalent in the case of the *Heliophanus* sp., which was most abundant at termite densities below 5%, but absent at high termite densities ($> 45\%$).

The five *Ammoxenus amphalodes* Dippenaar & Meyer 1980 (Ammoxenidae) specimens were all collected from mounds secondarily occupied by *H. mossambicus* ($n = 6$). As these spiders are known to be specialist predators of *H. mossambicus* (Dippenaar-Schoeman, et al. 1996 a, b), secondary occupation of these abandoned mounds by this termite is likely to be coupled with the presence of these spiders.

Spiders are among the most common and diverse groups of invertebrates colonizing abandoned *T. trinervoides* termite mounds. The height and degree of surface degradation of the mounds, and the presence of cavities in the mound structure are some of the factors influencing spider diversity and abundance. Spiders are possibly the most common and frequently encountered invertebrate predators inhabiting abandoned mounds.

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