

Coexistence of *Ammoxenus* (Gnaphosidae) spider species on and between termitaria of *Microhodotermes viator* (Hodotermitidae) at a Karoo site

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Previous studies of some species of *Ammoxenus* spiders demonstrated them to be monophagous predators of certain termites. Upon observing *Ammoxenus* spiders preying on the hodotermitid, *Microhodotermes viator*, we examined the distribution of spiders on or off termitaria (termed *heuweltjies*) at the Tierberg-LTER study site in the Karoo using pitfall traps deployed monthly over two years. Four species of *Ammoxenus* were found, but only one, *Ammoxenus pentheri*, has been described, the other three being new to science. Their coexistence prompts questions concerning niche partitioning among several specialist predators. Our initial study revealed that *Ammoxenus* and other ground spiders were more abundant on *heuweltjies* than in the matrix between *heuweltjies*. The different *Ammoxenus* species appeared to be disparately associated or disassociated with *heuweltjies* and had different phenologies. This case of niche partitioning among specialist predators warrants further study.

Ammoxenus spiders (Gnaphosidae) are free-living soil dwellers (Dippenaar-Schoeman et al. 1996a) usually found in the soft soil dumps left after excavation by the termites close to the nest entrance (Dippenaar-Schoeman and Harris 2005). The genus is endemic to southern Africa and presently known from six species (Dippenaar and Meyer 1980) but several new species await description (Bird 2003). They are very active spiders, usually found in areas with a high termite presence, running rapidly over the soil surface, moving between foraging termites and even entering tunnels of termite nests (van den Berg and Dippenaar-Schoeman 1991). All *Ammoxenus* species studied can dive head-first into the sand, using specialised setae on the chelicerae as digging apparatus, while the legs are kept close to the body as the spider pushes into the sand (pers. obs.). They construct sac-like silk retreats in soil mounds where they rest while not foraging.

Harvester termites forage mainly on grass, leaves, fine twigs and organic litter in the field outside their nests and are thus exposed to terrestrial predators. Among these predators are *Ammoxenus* spiders, invariably found near termite tunnel portals (Wilson and Clark 1977; Dippenaar and Meyer 1980; Dean 1988; van den Berg and Dippenaar-Schoeman 1991; Dippenaar-Schoeman et al. 1996a, b; Dippenaar-Schoeman and Harris 2005; Petrakova et al. 2015; Haddad et al. 2016). During prey capture, the spider grabs a termite, immobilises it by biting between its head capsule and the thorax, and drags the termite into the soil where the spider starts feeding (Dippenaar-Schoeman et al. 1996a, b; Dippenaar-Schoeman and Harris 2005; Petrakova et al. 2015).

Petrakova et al. (2015) provided the first solid evidence of *Ammoxenus* spiders being true monophagous predators. They used Next Generation Sequencing for molecular analysis of the gut contents of *Ammoxenus amphalodes* Dippenaar and Meyer comparing them to sequences of available prey in a grassland habitat. Their results showed that 99.8% of the extracted sequences belonged to *Hodotermes mossambicus* (Hagen) (Hodotermitidae), southern harvester termites. Dippenaar-Schoeman et al. (1996a) reported *Ammoxenus coccineus* Simon preying on snouted harvester termites *Trinervitermes trinervoides* (Sjöstedt) (Termitidae: Nasutitermitidae), indicating that different *Ammoxenus* species may specialise on different termites. The difference here is that *A. coccineus* must forage in soft sand near the termitaria, which are hard and impenetrable for *Ammoxenus* digging. *Ammoxenus* spiders were also reported preying on southern harvester termites *Microhodotermes viator* (Latreille) (Hodotermitidae) (Dean 1988) at Tierberg in the Karoo of the Western Cape. The four *Ammoxenus* species sampled there were included in a taxonomic revision by Bird (2003) and three species were identified as new to science. The unpublished results of Bird's (2003) revision indicated the presence of several sympatric species from Tierberg (Dippenaar-Schoeman et al. 2022) as well as sites near Hopetown, Kimberley and Cederberg (Foord et al. 2016).

The different *Ammoxenus* species were recorded at Tierberg-LTER (33.165461° S, 22.267926° E), a research site established in 1987 in a fenced livestock enclosure of 100 ha near Prince Albert in the Western Cape (Milton et al. 1992; Arena et al. 2018). The only termites recorded at this site are *M. viator* and *Amitermes* sp. (Termitidae: Termitinae) (Milton and Dean 1996) and *Psammotermes allocerus* Silvestri (Rhinotermitidae) (pers. obs.). However, the site is located within the broad

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distribution ranges also of *Angulitermes* sp. and *Microcerotermes* sp. (Termitidae: Termitinae), and *Fulleritermes mallyi* (Fuller) (Termitidae: Nasutitermitinae) (Uys 2002). It is unknown whether the Tierberg *Ammoxenus* spp. eat any termites other than *M. viator*. The sympatric occurrence of several species of *Ammoxenus* on 100 ha of semi-arid Karoo prompts the question of whether all of these *Ammoxenus* species are as strictly monophagous as found in previous studies (Dippenaar and Meyer 1980; Dippenaar-Schoeman et al. 1996a; Petrakova et al. 2015). If so, do the different *Ammoxenus* species prey on different termite species? Our data do not allow testing this for *Ammoxenus* but such segregation was found to be the case in sympatric termitophagous *Stenaelurillus* species (Salticidae) by Pekar et al. (2021).

However, it is possible to cast some light on a possible alternative hypothesis, namely that different *Ammoxenus* species specialise in different spatial and/or temporal niches of *M. viator* availability as prey at or away from their termitaria. Although the different morphospecies of *Ammoxenus* were identified from voucher specimens usually combined for both habitats (Bird 2003; Dippenaar-Schoeman et al. 2022), it was possible to examine the seasonal occurrence of *Ammoxenus* at the generic level in different habitats, following the approach used by Dean and Griffin (1993) for solifuges and Arena et al. (2020) for ants from the same dataset. The two habitats investigated in this study are defined by distinct patchiness due to the presence of 250 evenly-spaced 5–13 m wide termitaria of *Microhodotermes viator*, low mounds commonly called *heuweltjies*, which differ in terms of plant community composition and density, water infiltration rates, soil characteristics and biodiversity from the surrounding vegetation on the plains, or the matrix between the termitaria (Armstrong and Siegfried 1990; Milton and Dean 1990; Dean 1992; Milton et al. 1992).

From mid-1987 to mid-1990, pitfall trapping was conducted within the Tierberg enclosure for 24-h periods. Here we analyse the most consistent records during the final 24 months between July 1988 and June 1990, amounting to 960 trap days. The annual precipitation from July 1988 to June 1989 was 252 mm and 263 mm from July 1989 to June 1990, markedly higher than the long-term mean annual precipitation of 177 mm at Tierberg (Arena et al. 2018). Tin cans of 90 mm diameter were placed into the soil with the top rim flush with the ground surface. One trap was positioned on each of 20 *heuweltjies*. Another 20 traps were placed in a 5 × 4 grid, 20 m apart from each other on the plains (matrix). Field records separated *Ammoxenus* spp. from all other spiders combined, later identified by Dippenaar-Schoeman et al. (2022). Voucher specimens were deposited in the National Collection of Arachnida at the Agricultural Research Council, Pretoria. Pitfall-trapped *M. viator* were also recorded to indicate their availability as potential prey in the two habitats in different months. We compared the number of *Ammoxenus* spiders, collectively all other ground spiders, and *M. viator*, trapped monthly at *heuweltjies* and the matrix (*t*-test) and tested possible relationships of these variables with rainfall using linear regression. We also tested for correlations between *Ammoxenus* abundance and termite abundance (Pearson correlation) and presence or absence of termites (Mann–Whitney *U*-test). Statistical tests were performed using Statistica 7.1 with significance level set to 0.05.

During the current study period, the pitfall traps captured 725 spiders of 40 identifiable taxonomic categories (Dippenaar-Schoeman et al. 2022), with *Ammoxenus* spp. constituting 51.3% of the catch (67 *Ammoxenus pentheri* Simon; 251 sp. 1; 44 sp. 2; 6 sp. 3; 4 undetermined). *Ammoxenus* numbers were not significantly correlated with termite numbers ($r = 0.25$; $p > 0.5$), nor with the presence or absence of termites (Mann–Whitney: $U_{22,26} = 250$; $p > 0.05$). There was no correlation, not even when

lagged, between the occurrences of *Ammoxenus* and *M. viator* ($r < 0.37$). The abundances of ammxoenids and other spider taxa in both habitats were unrelated to the rainfall pattern (Figure 1; $r^2 < 0.051$). The only common seasonal pattern was that fewer spiders were recorded during winter than during the spring and summer months of October to March.

Overall, *Ammoxenus* were more abundant on *heuweltjies* than the matrix (206 vs 166), although the monthly abundances were strongly correlated between habitats ($r = 0.93$). Due to high variability, differences in the mean monthly abundances of *Ammoxenus* on and off the *heuweltjies* were not significant (mean abundance over the trapping period: 8.2 ± 12.1 vs 6.6 ± 9.6 ; $t_{24} = 1.70$, $p > 0.05$; Figure 1). However, “other spiders” were, on average, significantly more abundant on the *heuweltjies* than in the matrix (8.9 ± 5.7 vs 5.3 ± 3.9 ; paired- $t_{24} = 3.6$, $p < 0.002$; $r = 0.53$; Figure 1). Monthly records of *Ammoxenus* were strongly correlated with those of other spiders on the *heuweltjies* ($r = 0.72$, $p < 0.05$) but not on the matrix ($r = 0.20$). There was no significant difference in the highly variable numbers (CV = 300%) or frequency of *M. viator* occurrences in traps between habitats ($p > 0.05$; Figure 1).

The three *Ammoxenus* species had different seasonal activities (Figure 2, Table S1); the fourth species was uncommon ($n = 6$) and seasonal data could not be generated. The most abundant species, *Ammoxenus* sp. 1, was most active in summer, December to February and least during winter, June to August. The bulk of the captures (54%) were adult males. During the peak season, the sex ratio was strongly skewed at 4.61♂:1♀ ($\chi^2_1 = 42.3$, $p < 0.001$). Some 29% of the voucher specimens were accompanied by habitat data, all referring to *heuweltjies*. It can therefore be assumed that *Ammoxenus* sp. 1 is most strongly associated with termitaria. By contrast, 94% of *Ammoxenus pentheri* were recorded during spring, September to November (Figure 2), with the sex ratio of 1.53♂:1♀ not significantly skew. None of these records indicated *heuweltjie* habitat, and it can be assumed that *A. pentheri* is associated with the matrix. A third species, *Ammoxenus* sp. 2, was also most active during spring (48%), but this species was recorded throughout the year (Figure 2) with a skew sex ratio (3.14♂:1♀, $\chi^2_1 = 42.3$, $p < 0.005$). Only one record was from a *heuweltjie*. Too few *Ammoxenus* sp. 3 (3♂, 2♀, 1 juv.) were recorded to analyse.

Our observations indicate that *Ammoxenus* and other ground spiders were more abundant or active at *heuweltjies* than in the matrix, just as previously recorded for web spiders (Henschel and Lubin 2018). *Ammoxenus* spp. and *M. viator* were occasionally recorded on and off *heuweltjies*. These termites forage irruptively across the entire area, emerging from foraging portals (Figure 3) on or up to tens of metres from the termitaria to collect plant matter. However, their foraging events are highly sporadic and unpredictable, making it difficult for predators to track the appearance of termites foraging on the surface (Dean 1993).

Pitfall traps are probably ill-suited to track the swarms of *M. viator* during their brief appearances on the surface (Southwood 1978) but may perhaps catch the odd foraging scout. Pitfall traps would also be unlikely to collect the termites when they emerge over very short distances at ejecta portals to push out frass and other debris from their nest. However, the frequent appearance of termites at the ejecta portals may enable *Ammoxenus*, waiting on the frass heaps, to capture them, as do several other predators such as *Eurychora* sp. (Coleoptera: Tenebrionidae), crabronid wasps (Hymenoptera), spiders, birds, lizards and small mammals (pers. obs.). Although prey availability at frass heaps would be more predictable, given the daily activities of termites at certain ejecta portals for weeks to months on end (pers. obs.), predators and prey are probably difficult to detect with pitfall traps due to the short distances moved. Also, arthropod predators face several risks at ejecta portals. Termite soldiers may injure *Ammoxenus*,

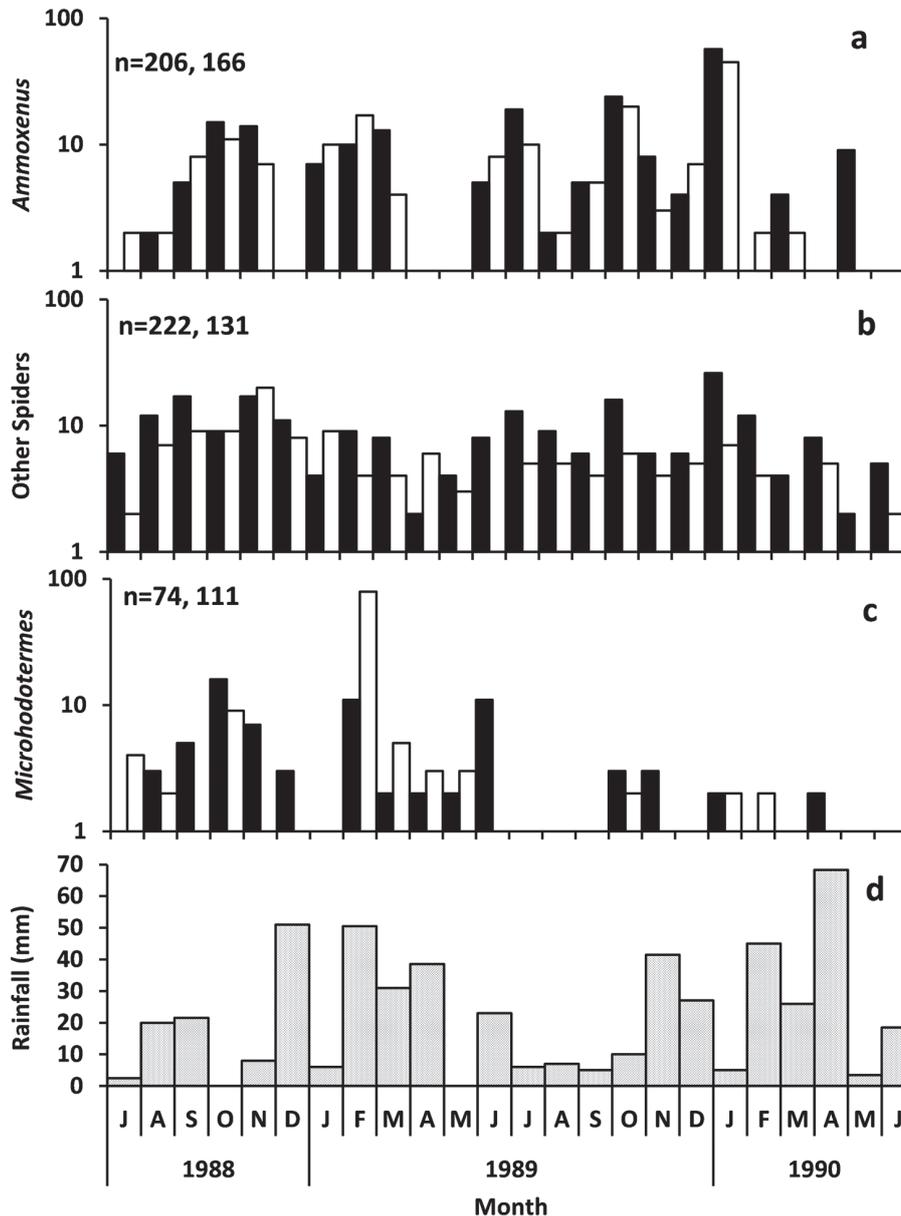


Figure 1. Number of *Ammoxenus* spp., other spiders and *Microhodotermes viator* recorded during different months in pitfall traps on heuweltjies (dark) and matrix (light), in comparison to monthly rainfall (shaded) over the 24 study months

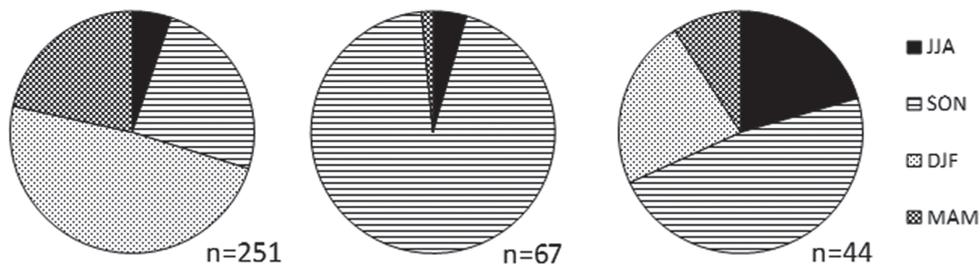


Figure 2. Proportion of records from Tierberg-LTER between July 1988 to June 1990 of *Ammoxenus* sp. 1 (left), *Ammoxenus pentheri* (middle), and *Ammoxenus* sp. 2 (right) in different seasons, indicated by month acronyms

but with these spiders' ability to burrow themselves they are usually able to escape predators, and vertebrate predators such as birds and lizards may also capture the spiders (pers. obs.). The observation at Tierberg of a swarm of *M. viator* termites attacking a theraphosid spider and driving it out of its burrow by day reflects risks for burrowing spiders at termitaria, even when not hunting (Henschel and Jürgens 2022).

Conditions are different for *Ammoxenus* on the matrix, where these spiders can only wait for termite irruptions from foraging portals whenever and wherever they occur (Dean

1988). The density of foraging portals diminishes with distance from termitaria due to the termites' central place foraging patterns (Laurie 2002). *Ammoxenus* waiting for surface-active *M. viator* midway between heuweltjies would therefore experience slimmer resource levels than those on or near heuweltjies. Nevertheless, as soon as termites emerge from the foraging portals, *Ammoxenus* spiders emerge from soil mounds or soft soil around these portals (Dippenaar-Schoeman et al. 1996a). Laboratory observations have shown that *A. amthalodes* and *A. pentheri* can readily detect the presence of termites,



Figure 3. A foraging portal of *Microhodotermes viator* with unretrieved old food (a) and an ejecta portal with dark fresh frass and debris and termites (b)

and the spiders immediately surface after termites have been introduced into their containers (Dippenaar-Schoeman et al. 1996a). In the field, their presence near foraging holes apparently enables them to detect termite foraging activity, perhaps through soil vibrations or chemical cues. Wilson and Clark (1977) have shown that *A. daedalus* can detect termite activity throughout a 24-hour period in the field and that the spiders adapt their activity pattern to that of *H. mossambicus*. The same may be true for Tierberg with *Ammoxenus* foraging for *M. viator*.

The binary recording of habitat (either heuweltjie or matrix) in our study does not allow for more refined analyses besides noting that *Ammoxenus* were overall more abundant on heuweltjies than off. The different *Ammoxenus* species at Tierberg may perhaps utilise different niches represented by decreasing resource levels with increasing distances from the termitaria, enabling sympatry of monophagous species with different traits. Perhaps *Ammoxenus* sp. 3, which was seldom recorded in our study, was more abundant in habitats that were not sampled, such as among the nearby riparian vegetation. Additionally, as diet was not tested, one or more of these species might be preying on other species of termites, just as *A. coccineus* preys on nasutitermitine termites (Dippenaar-Schoeman et al. 1996a).

Our findings indicate that there may be spatiotemporal separation of species. The numerically dominant species, *Ammoxenus* sp. 1, appears to be most closely associated with heuweltjies, while *Ammoxenus pentheri* may avoid heuweltjies, and *Ammoxenus* sp. 2 is perhaps intermediate, at the heuweltjie margins. Differences in phenology regarding seasonal activity and maturity patterns further separate these species even though they may specialise on the same prey. These conclusions require confirmation, including elucidating the alternative hypothesis concerning the possibility that these sympatric monophagous predators could be hunting different prey.

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AUTHOR CONTRIBUTION

JRH: Formal Analysis, Writing – Original Draft; WRJD: Conceptualisation, Data Curation, Investigation, Methodology, Project Administration, Resources; SJM: Data Curation, Funding Acquisition, Writing – Review and Editing; ASD: Data Curation, Investigation, Writing – Review and Editing

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