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Seasonal population dynamics of a specialized termite-eating spider (Araneae: Ammoxenidae) and its prey (Isoptera: Hodotermitidae)

Charles Richard Haddad[a,*], Marek Brabec[b], Stano Pekár[c], René Fourie[a,1]

[a] Department of Zoology & Entomology, University of the Free State, P.O. Box 339, Bloemfontein 9300, South Africa
[b] Department of Nonlinear Modelling, Institute of Computer Science, The Czech Academy of Sciences, Pod Vodarenskou vezi 2, Praha 8, 182 07 Prague, Czech Republic
[c] Department of Botany and Zoology, Faculty of Sciences, Masaryk University, Kotlářská 2, 611 37 Brno, Czech Republic

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ABSTRACT

Specialized predators should be adapted spatially and temporally to the occurrence and abundance of their exclusive prey. Several spider species have specialized to feed on prey that is highly aggregated, including ants and termites. *Ammoxenus* (Araneae: Ammoxenidae) are spiders that are specialist predators of harvester termites in southern Africa. Epigeal spiders and termites were sampled by pitfall trapping from six sites in the Erfenis Dam Nature Reserve, South Africa, over a period of one year. We found *Ammoxenus amphalodes* Dippenaar & Meyer, and two termite species, *Hodotermes mossambicus* (Hagen) (Isoptera: Hodotermitidae) and *Trinervitermes trinervoides* (Sjöstedt) (Isoptera: Termitidae) to be abundant there. Our data show that *A. amphalodes* is a univoltine species with a wide reproductive period corresponding to the seasonal occurrence of termites. The activity density of *A. amphalodes* was tightly coupled to the activity density of *H. mossambicus*, but not to that of *T. trinervoides*. These data provide further evidence that *A. amphalodes* is a monophagous true predator. However, its role as a biocontrol agent against termites is limited due to an insufficient numerical response.

1. Introduction

Spiders are the most diversified true predators (*sensu* Begon et al., 1996) in terrestrial ecosystems (Coddington and Levi, 1991). The majority of spider species are polyphagous generalist predators (Pekár et al., 2011), but several species from a few families have specialized on one of six prey types: ants, termites, spiders, woodlice, moths and flies (Pekár and Toft, 2015). With the exception of flies, the former prey types are well protected by aggressive or defensive behavior, chemical or morphological defense, and social organization, and are therefore often avoided by many generalist predators. Specialized predators have evolved adaptations that increase the efficiency of prey capture and processing (Pekár and Toft, 2015). The advantages of specialization are lower competition from other generalist predators and access to (often) highly abundant food sources (Nentwig, 1986). This is in agreement with the optimal foraging theory, which predicts that increasing prey food abundance leads to greater prey food specialization (Pyke et al., 1977).

Termite societies provide spatially high concentrations of prey, which is the reason why several animals, from arthropods to mammals, have taken the opportunity and became (facultatively) termitophagous (Sheppe, 1970; Wesołowska and Haddad, 2002). Natural predators of termites include lizards, birds, mammals, and a variety of arthropods (Dippenaar-Schoeman et al., 1996a), among which Sheppe (1970) observed ants to be the most important. Other termitophagous arthropod predators include beetles (Coleoptera: Staphylinidae: *Zyras*), true bugs (Reduviidae), phasmids, centipedes, and spiders (Nel, 1970; Sheppe, 1970).

Fifty-four termite genera in five families have been recorded from southern Africa (Uys, 2002). Only a couple of them, such as the genera *Trinervitermes* (Termitidae), *Microhodotermes* and *Hodotermes* (both Hodotermitidae), are harvesters, foraging mainly on grass, leaf litter and other non-woody material, and are thus exposed to terrestrial predators. Harvester termites have been considered one of the major pests of grasses in managed rangelands in South Africa, particularly in areas with an annual water shortage (Nel, 1967; Mitchell, 2002). The damage to rangelands appears only to be important when stresses of some kind (over-grazing, drought etc.) have led to very poor productivity.

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[*] Corresponding author. Fax: +27 51 401 9950.
E-mail addresses: haddadcr@ufs.ac.za, africanspiders@gmail.com (C.R. Haddad).

[1] Present address: Quintiles International, Nelson Mandela Drive, Bloemfontein 9301, South Africa.

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Trinervitermes species build extensive polycalic nests, with single subterranean nests usually subtended on the surface by numerous dome-shaped mounds (Nel and Malan, 1974; Uys, 2002). Hodotermitids have soil dumps on the soil surface and underground nests with a network of galleries (Nel and Hewitt, 1969; Heidecker and Leuthold, 1984; Uys, 2002). Harvesting takes place usually once a day for a period of a couple of hours, either during the day or at night (Nel, 1970; Leuthold et al., 1976; Heidecker and Leuthold, 1984).

Several spider species from various families (Ammoxenidae, Gnaphosidae, Philodromidae, Salticidae, Thomisidae, Theridiidae, and Zodariidae) have been commonly found associated with different termite species (e.g. Eberhard, 1991; Van den Berg and Dippenaar-Schoeman, 1991; Dejean and Bolton, 1995; Dippenaar-Schoeman et al., 1996a,b; Wesołowska and Cumming, 1999, 2002; Haddad and Dippenaar-Schoeman, 2002, 2006; Wesołowska and Haddad, 2002; Haddad and Wesołowska, 2006; De Visser et al., 2008; Marshall et al., 2015). Some species are only termitophilous (permanently residing in the termite mound), while others also prey on their hosts. Recent stable isotope analysis suggests that spiders are the top predators of the invertebrate food web located within active termitaria, but that they rarely feed on the termites themselves directly (De Visser et al., 2008).

Among Ammoxenidae, species of the genus *Ammoxenus* are specialist predators of harvester termites. Ammoxenid spiders are free-living soil dwellers (Dippenaar-Schoeman et al., 1996b) usually found in the soft soil dumps left after excavation by the termites in close proximity to the nest entrance (Dippenaar-Schoeman and Harris, 2005). They are very active spiders, running rapidly over the soil surface, moving between foraging termites and even entering tunnels of termite nests (Van den Berg and Dippenaar-Schoeman, 1991). During prey capture, the spider grabs the termite, bites it between its head capsule and the thorax, after which the dead termite is dragged underneath the soil before the spider starts feeding (Dippenaar-Schoeman et al., 1996b; Dippenaar-Schoeman and Harris, 2005; Petráková et al., 2015). They construct sac-like silk retreats in the soil mounds where they rest while not foraging.

Recent analysis of the natural prey of *Ammoxenus amphalodes* Dippenaar & Meyer by means of gut content detection using molecular methods revealed that they only feed on *Hodotermes mossambicus* (Hagen) termites (Petráková et al., 2015). Subsequent laboratory acceptance experiments with adults and juveniles of *A. amphalodes* individuals showed that the spiders did not catch other arthropods or other termite species. Altogether, these data provided strong evidence for monophagy in *A. amphalodes* (Petráková et al., 2015).

Our aim in this study was to find out which termite(s) *A. amphalodes* exploits when multiple termite species co-inhabit a particular environment. We predicted that if *A. amphalodes* exploits a particular termite species then it should have coupled population dynamics with its prey. Furthermore, we predicted that it should be reproductively adapted to the occurrence of its prey. Thus, we sampled *A. amphalodes* spiders and epigeic harvester termites at several sites in a nature reserve over the course of a year and used statistical models to detect density-dependence in population dynamics.

2. Materials and methods

2.1. Study area and sampling methods

The Erfenis Dam Nature Reserve is located in the central part of the Free State Province, South Africa, south-east of Theunissen. The dam is part of the Vet River system and the reserve extends about 4000 ha, of which 3300 ha comprises the dam and the remaining 700 ha grassland (Hugo-Coetzee and Avenant, 2011).

Pitfall trapping was used to sample cursorial invertebrates in the reserve as part of a study of the impacts of a fast-burning spring fire on invertebrate communities (Haddad et al., 2015). While the focus of this study was to investigate the effects of burning on spider assemblages, the potential was seen to study the relationships between *A. amphalodes* and potential termite prey, as solid data on the activity densities of these arthropods could be easily generated. The study was initiated at the end of September 2005, the day following the burning, and continued for the duration of a year. As termites were not retained from the first month's sample of the burn study (October 2005), an additional month's sampling was conducted in October 2006 to generate twelve months' overlapping data on *A. amphalodes* and termite activity density. Thus, the data analyzed in the present study covered the period from November 2005 to October 2006. February had the second highest rainfall of that year. This led to the loss of six of the 60 pitfall traps used in the survey, which were immediately replaced.

Ten pitfall traps (diameter 8 cm) were set out per site in six different localities (Appendix A), with three sites located within a single continuous burned area and the other three sites in the unburned area (see Haddad et al., 2015 for further site details). Intersite distances were calculated using the path measurement tool in Google Earth Pro and are provided in Supplementary Table 1 (Appendix A). Sites were a minimum of 190 m apart. Pitfall traps were used because they exclusively sample ground-active arthropods continuously during the day and night. Burned sites 1–3 were located 50 m from the western and eastern margins of the fire, respectively, and all three burned sites were 50 m from the southern fire margin. Unburned site 1 was 50 m east of the eastern fire margin, and unburned sites 2 and 3 were located on the opposite side of the dam. Traps were arranged in a 5×2 grid at each site, with 5 m separating each trap. The traps were buried level with the upper ground surface, and 100 ml of ethanediol was added as a preservative. The traps were left exposed for 30 days before being emptied. The spiders and termites that were caught in the traps were removed and preserved in 70% ethanol.

Following sorting and identification of spiders in the laboratory, the activity density of different life stages (juveniles, adult males and females) of *A. amphalodes* at the six sites was noted. The termites that were collected were also removed and identified as two species, *H. mossambicus* and *Trinervitermes trinervoides* (Sjöstedt). The activity density of the two species at the six sites, as well as the castes of individual termites, was determined.

2.2. Statistical analysis

To fit the predator–prey seasonal dynamics we used Generalised Linear Mixed Models (GLMM) model class using the mgcv package (Wood, 2006). The statistical modeling aimed at addressing several questions about the *Ammoxenus* dynamics, namely: (i) is the count of *Ammoxenus* influenced by rainfall or not?; (ii) how important are different prey species (*Hodotermes*, *Trinervitermes*)?; (iii) is the influence of prey number (either *Hodotermes*, or *Trinervitermes*) linear (on the scale of intensity) or not?

To this end, we fitted models with *Hodotermes* and *Trinervitermes* counts, rainfall volume and random effect of location in the linear predictor. Since we worked with Poisson or negative-binomial models and canonical (log) link, it is natural to use logarithm of a covariate (*Hodotermes* and *Trinervitermes* counts, rainfall volume). Since we are modeling log-intensity, logarithm of a covariate corresponds to assuming usual power relationship on the scale of intensity. To assess potential nonlinearity on log-intensity scale