Soil Biology & Biochemistry 38 (2006) 2985–2989

Soil Biology & Biochemistry

www.elsevier.com/locate/soilbio

Short communication

Do oribatid mites live in enemy-free space? Evidence from feeding experiments with the predatory mite *Pergamasus septentrionalis*

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Received 17 March 2006; received in revised form 14 April 2006; accepted 19 April 2006
Available online 19 May 2006

Abstract

To examine whether their strongly hardened cuticle permits adult oribatid mites (Acari) to live in enemy-free space, we investigated (1) if *Pergamasus septentrionalis*, a widespread and abundant predatory mesostigmate mite species, is able to feed on oribatid mites, (2) if this predator preferentially feeds on certain oribatid mite species and (3) to what extent oribatid mites are consumed compared to collembolans and juvenile Mesostigmata. Single adult individuals of six different oribatid mite species (*Steganacarus magnus*; *Nothrus silvestris; Damaeus riparius*; *Liacarus coracinus; Eupelops plicatus*; *Achipteria coleoptrata*), one collembolan species (*Folsomia quadrioculata*) and juvenile *Pergamasus* spp. were offered separately to adult *P. septentrionalis* in a no-choice feeding experiment. The predators quickly and preferentially fed on collembolans and juvenile *Pergamasus*; three oribatid mite species were occasionally eaten (*L. coracinus, N. silvestris, A. coleoptrata*); the other oribatid mite species were rejected as food (*E. plicatus*, *S. magnus*, *H. riparius*). When preying on oribatid mites, *P. septentrionalis* typically first cut off the legs of the mite, then opened the body through the region of the genital plates or the mouthparts. The results suggest that predator pressure on adult oribatid mites in the field is low, since few relevant predators at the study site are more abundant and powerful than *P. septentrionalis*. Adult oribatid mites therefore likely indeed live in enemy-free space, i.e. are little affected by predators, but that may not apply to soft-bodied immatures. Collembolans were quickly consumed indicating that they comprise a major part of the diet of *P. septentrionalis*. Strong feeding on juveniles of *Pergamasus* suggests that *P. septentrionalis* also functions as an intra-guild predator.

Keywords: Cannibalism; Collembolans; Enemy-free space; Generalist feeding; Intra-guild predation; Mesostigmata; Oribatida

Oribatid mites are mostly soil living animals that predominantly feed on fungi and decomposing plant materials (Walter and Proctor, 1999; Maraun et al., 2003; Schneider et al., 2004) and reach high densities in virtually all soils of the world, often surpassing 100,000 m^{-2} (Wallwork, 1983; Maraun and Scheu, 2000). Most juvenile oribatid mites have a soft cuticle and therefore likely are susceptible to predation (Woodring and Cook, 1962; Luxton, 1966; Lebrun, 1970; Wallwork, 1983; Walter et al., 1987). By contrast, adults of most species have multiple traits that have been interpreted as predator defenses.

The adult cuticle of most species is hardened, either by sclerotization or mineralization (Norton and Behan-Pelletier, 1991) and often there are diverse cuticular formations (lamellae, tecta) that offer protection for legs or vulnerable articulations (Schmid, 1988). Other suggested morphological defences include special hairs or unusually thick extracuticular deposits (e.g. organic debris or waxy secretions), as well as a snail-like closure mechanism in several lineages having the ptychoid body form (Sanders and Norton, 2004). Most oribatid mites also possess opisthonotal glands that secrete noxious or toxic chemicals (Sakata and Norton, 2001; Raspotnig et al., 2003; Takada et al., 2005). Such defences may provide little protection against powerful predators such as amphibians (Norton and MacNamara, 1976; Maiorana, 1978; Kupfer and Maraun, 2003) ants (Masuko, 1994; Wilson, 2005), or scydmaenid (Schmid, 1988), ptiliid (Riha, 1951; Cancela da Fonseca, 1975) and pselaphid beetles (Park, 1947).

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0038-0717/$ - see front matter © 2006 Elsevier Ltd. All rights reserved.
doi:10.1016/j.soilbio.2006.04.035

However, their most abundant predators in soil presumably are other mites, in the taxa Prostigmata and Mesostigmata.

Information about the significance of predation on adult oribatids is anecdotal, but Norton (1994) suggested that selection pressure from predatory mites resulted in the diversity of oribatid defenses, some of which have been maintained since the Devonian and Carboniferous periods. If the current defenses are effective, and pressure from predatory mites is now low, then it can be hypothesized that adult oribatid mites currently live in 'enemy-free space,' (Jeffries and Lawton, 1984). We tested this idea using a mite predator in the taxon Mesostigmata.

Most soil living Mesostigmata (Acari: mainly Dermanyssina and Parasitina) are aggressive predators of soil animals, including collembolans, mites, enchytraeids and nematodes. They actively search for prey (Walter and Oliver, 1990) and occasionally hunt in groups (Usher and Davis, 1983; Walter and Proctor, 1999). At least some Mesostigmata feed on juveniles of other Mesostigmata (intra-guild predation; Polis et al., 1989) and when food is scarce some also consume their own offspring, i.e. are cannibalistic (Lindquist and Walter, 1989). The degree of food specialization of predatory soil mites is little known but it has been suggested that, as is typical of soil predators, many are generalist rather than specialist predators (Woodring and Cook, 1962; Scheu and Setälä, 2002). Generalist predators may contribute to the high diversity of soil animals if generalist feeding reduces interspecific competition among prey species (Paine, 1966).

The antagonist subject of our experiments was one of the largest and most active species of predatory soil Mesostigmata, *Pergamasus septentrionalis* (Oudemans) of the family Parasitidae, which is common and abundant in forest soils of northern Europe and eastern North America. It is a generalist predator proven to feed on collembolans, nematodes, dipteran larvae, pseudoscorpions, aphids, psocopterans, other mesostigmatans (including conspecifics) and a variety of oribatid mites (Hartenstein, 1962; Karg, 1993). We tested if *P. septentrionalis* prefers selected soft-bodied soil animals to adult oribatid mites, and determined how quickly particular prey are attacked and consumed under laboratory conditions.

All study organisms, mites and collembolans, were collected from litter (L and F material) of an oak-beech forest (Kranichsteiner Wald) close to Darmstadt using heat-extraction (Kempson et al., 1963). In the region of Darmstadt winters usually are mild and summers humid; the annual precipitation is about 700 mm and the mean temperature 9.5 °C. Parent rock at the study site is Cisuralian (Rotliegendes; Early Permian) and the soil is an orthic luvisol including Holocene alluvial loams and loess. The soil type is a typical moder with a pH of 3.6–4.3. Oak trees (*Quercus robur* L.) dominate and beech (*Fagus sylvatica* L.) and hornbeam (*Carpinus betulus* L.) are interspersed. In a series of no-choice feeding experiments, one adult predator (*P. septentrionalis*) and one individual of a potential prey species were placed in a circular plastic box (diameter 3.5 cm) closed with a perspex lid. The bottom of the boxes was covered with moist filter paper. A piece of beech litter of about 4 cm^2 was added to provide shelter. Oribatid mites offered as prey included adults of *Steganacarus magnus* (Nicolet), *Nothrus silvestris* Nicolet, *Damaeus riparius* Nicolet, *Liacarus coracinus* (Koch), *Eupelops plicatus* (Koch) and *Achipteria coleoptrata* (Linnaeus). *Folsomia quadrioculata* (Tullberg) represented the Collembola, and unidentified juveniles of at least two *Pergamasus* spp. represented intra-guild prey. For each of the eight prey types, seven replicates were set up at room temperature under natural light conditions. Survival of the predator and prey was recorded daily for 30 days. Data on survival of prey taxa at the end of the experiment were analysed by Kruskal–Wallis test using STATISTICA 7.1 (Statsoft Inc., Tulsa, USA). The fixed factor was 'food type' and the dependent factor was 'survival after 30 days'.

P. septentrionalis adults fed with different intensities on the offered prey (Kruskal–Wallis test: $H_{7,49} = 31.47$, $P < 0.0001$); at the end of the experiment all collembolans and 6 of the 7 individuals of juvenile *Pergamasus* spp. had been consumed. Of the oribatid mites, 4, 3 and 2 individuals of *L. coracinus*, *N. silvestris* and *A. coleoptrata* were consumed, respectively. No individual of *S. magnus*, *E. plicatus* or *D. riparius* was consumed (Fig. 1). Survival of collembolans and juvenile *Pergamasus* spp. differed significantly from that of *E. plicatus, S. magnus* and *D. riparius*. In treatments with oribatid mites, *P. septentrionalis* individuals often died before the end of the experiment.

Enemy-free space, as defined by Jeffries and Lawton (1984), is a conceptual condition resulting from "ways of living that reduce or limit a species' vulnerability to one or more species of natural enemies". Considering only predators, our study supports the hypothesis that adults of some oribatid mites may live in nearly enemy-free space and some others are probably under only low predation pressure. Except for two individuals of *N. silvestris*, no tested oribatid mite was killed in less than 15 days of constant exposure to a predator—in this case one of the largest and most agile generalist predators in soil—with no other prey present. By contrast, no collembolan survived more than 3 days, and all but one juvenile *Pergamasus* were killed within 13 days.

Prey that was most rapidly consumed—collembolans and *Pergamasus* juveniles—move much more quickly than do oribatid mites, suggesting that cuticular hardening was the principal deterrent. Prey were consumed in the order: collembolans > juvenile *Pergamasus* > *N. silvestris* > *L. coracinus* > *A. coleoptrata*; this is exactly the order of increasing cuticular defense, in terms of apparent strength of sclerotization and the formation of complex tecta. Of the oribatid mite species that were never consumed, all have hard cuticles. That of *S. magnus* is strongly hardened by calcium carbonate, while both *E. plicatus* and *D. riparius* have not only well-sclerotized cuticle but also a strongly