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SHORT NOTE

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Oribatid mite (Acari, Oribatida) feeding on ectomycorrhizal fungi

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Abstract The coexistence of a large number of soil animals without extensive niche differentiation is one of the great riddles in soil biology. The main aim of this study was to explore the importance of partitioning of food resources for the high diversity of micro-arthropods in soil. In addition, we investigated if ectomycorrhizal fungi are preferentially consumed compared to saprotrophic fungi. Until today, ectomycorrhizal fungi have never been tested as potential food resource for oribatid mites. We offered six ectomycorrhizal fungi [*Amanita muscaria* (L.) Hook., *Boletus badius* (Fr.) Fr., *Cenococcum geophilum* Fr., *Laccaria laccata* (Scop.) Fr., *Paxillus involutus* (Batsch) Fr. and *Piloderma croceum* J. Erikss. & Hjortstam], one ericoid mycorrhizal fungus [*Hymenoscyphus ericae* (D.J. Read) Korf & Kernan] and three saprotrophic fungi [*Agrocybe gibberosa* (Fr.) Fayod, *Alternaria alternata* (Fr.) Keissl. and *Mortierella ramanniana* (A. Møller) Linnem.] simultaneously to each of the mainly mycophagous oribatid mite species *Carabodes femoralis* (Nicolet), *Nothrus silvestris* Nicolet and *Oribatula tibialis* Nicolet. The ericoid mycorrhizal fungus *H. ericae* and the ectomycorrhizal fungus *B. badius* were preferentially consumed by each oribatid mite species. However, feeding preferences differed significantly between the three species, with *O. tibialis* being most selective. This study for the first time documented that oribatid mites feed on certain ectomycorrhizal fungi.

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Introduction

Micro-arthropods are among the most abundant decomposers in soil. Oribatid mites (Acari, Oribatida), as part of the micro-arthropod community, reach densities of up to 400,000 individuals/m^2 in temperate forests. They comprise about 10,000 described species worldwide (Schatz 2002), of which 550 occur in Germany (G. Weigmann, personal communication). Wunderle (1992) found 119 oribatid mite species in a temperate beech forest in Germany. Surprisingly, it is still unknown how this large number of species can coexist with no clear and obvious niche differentiation (Anderson 1975).

Limited evidence for trophic niche differentiation has been found in studies on gut content, cheliceral size and enzyme activity in the gut of oribatid mites (Schuster 1956; Luxton 1972; Kaneko 1988; Siepel and de Ruiter-Dijkman 1993). In contrast, Schneider et al. (2004) documented strong trophic niche differentiation in oribatid mites using stable isotopes (^{15}N). Food choice experiments indicated a general preference for dark pigmented fungi (“Dematiacea”; Maraun et al. 1998). Therefore, Schneider and Maraun (2005) coined the term “choosy generalists” for oribatid mites, since they generally have a wide food spectrum but feed selectively when high-quality food is available.

Fungal grazing by micro-arthropods affects microbial respiration (Bengtsson and Rundgren 1983; Kaneko et al. 1998), decomposition rates (Cortet et al. 2003), nutrient cycling (Bonkowski et al. 2000), plant growth (Klironomos and Kendrick 1995; Gange 2000), fungal biomass (Hanlon and Anderson 1979; Bardgett et al. 1993), fungal succession (Visser 1985), the distribution of fungi in soils (Lussenhop 1992) and the interaction between competing fungal species (Tiunov and Scheu 2005). While grazing on saprotrophic fungi and arbuscular mycorrhizal (AM) fungi is well studied (Lussenhop 1992; Gunn and Cherrett 1993;

Larsen and Jakobsen 1996; Hopkin 1997; Klironomos and Moutoglis 1999; Sabatini and Innocenti 2000; Cole et al. 2004), the feeding on ectomycorrhizal fungi has hardly been investigated. This is surprising, since ectomycorrhizal fungi are common in soils (Read et al. 1992) and are probably of high nutritional value (Wolters 1985; Schultz 1991; Hopkin 1997). Furthermore, the interaction between soil micro-arthropods and ectomycorrhizal fungi may affect plant performance (Smith and Read 1997).

More often than oribatid mites, collembolans have been used to study effects of soil micro-arthropods on mycorrhizal fungi. *Proisotoma minuta* and *Onychiurus armatus* consumed a number of ectomycorrhizal fungi offered in laboratory food choice experiments (Shaw 1985, 1988; Hiol Hiol et al. 1994). Klironomos and Kendrick (1996) investigated the feeding preferences of six species of mites and collembolans for one AM fungus and two saprotrophic fungi and showed that they preferentially graze on hyphae of conidial fungi rather than on those of AM fungi. However, oribatid mite feeding on ectomycorrhizal fungi has never been studied.

This study for the first time investigates feeding preferences of oribatid mites for ectomycorrhizal fungi. Feeding preferences for ectomycorrhizal fungal species were compared with those for saprotrophic fungi. We hypothesized that oribatid mite species selectively feed on ectomycorrhizal fungi, which may partially explain how the large number of oribatid mite species can coexist.

Materials and methods

In April 2004 the oribatid mite species *Carabodes femoralis* (Nicolet), *Nothrus silvestris* Nicolet and *Oribatula tibialis* Nicolet were extracted by heat (Kempson et al. 1963) from the soil of a beech–oak forest near Darmstadt (Kranichsteiner Wald, Hesse, Germany). We chose these oribatid mite species because they mainly feed on fungi (Schneider et al. 2004).

Six ectomycorrhizal fungi, *Amanita muscaria* (L.) Hook., *Boletus badius* (Fr.) Fr., *Cenococcum geophilum* Fr., *Laccaria laccata* (Scop.) Fr., *Paxillus involutus* (Batsch) Fr. and *Piloderma croceum* J. Erikss. & Hjortstam, one ericoid mycorrhizal fungus, *Hymenoscyphus ericae* (D.J. Read) Korf & Kernan, and three saprotrophic fungi, *Agrocybe gibberosa* (Fr.) Fayod, *Alternaria alternata* (Fr.) Keissl. and *Mortierella ramanniana* (A. Møller) Linnem. (Table 1), were offered simultaneously to each oribatid mite species. The three saprotrophic fungal species were chosen because they ranked from high to low food quality (*A. alternata*, high; *M. ramanniana*, intermediate; and *A. gibberosa*, low; Ruess et al. 2000; Maraun et al. 2003; Schneider and Maraun 2005), and because we wanted to compare feeding preferences of oribatid mites on ectomycorrhiza with those on saprotrophic fungi. Fungal species were taken from cultures (Table 1) which were stored in the laboratory at 15°C. Ten weeks before the start of the experiment they were inoculated on Pachlewska agar, containing, per 1 l distilled water, 20 g glucose, 5 g maltose, 0.5 g $MgSO_4 \cdot 7H_2O$, 1 g KH_2PO_4, 0.5 g NH_4 tartrate, 50 µg thiamine HCl, 0.5 ml Fe citrate (1%), 0.5 ml $ZnSO_4$ (0.2%) and 15 g agar. Species names of the fungi are subsequently abbreviated as genera names.

Fungi were offered on small agar discs (8 mm Ø) which were cut out of the growing front of the fungal colonies and placed in a circle 5 cm in diameter in plastic vessels (7 cm Ø); this experimental design has been used previously in food choice experiments (Maraun et al. 1998; Schneider and Maraun 2005). The bottom of the vessels consisted of a layer of plaster of Paris. Five individuals of the respective oribatid mite species were placed in the centre of the vessels. After 3 weeks, faecal pellets deposited in close vicinity of the fungal agar discs were counted and taken as a measure of the amount of food consumed, i.e. feeding

Table 1 Taxonomic affiliation, trophic mode and source of the ten fungal species used in this study

Fungi	Trophic mode	Source
Zygomycota		
Mortierella ramanniana (Møller) Linnem.	Saprotroph	Leaf litter of the Kranichsteiner Wald (Hesse, Germany)
Ascomycota		
Alternaria alternata (Fr.) Keissl.	Saprotroph	Leaf litter of the Kranichsteiner Wald (Hesse, Germany)
Cenococcum geophilum Fr.	Ectomycorrhiza	Fungal culture of the University of Leipzig (Germany)
Hymenoscyphus ericae (Read) Korf and Kernan	Ericoid mycorrhiza	Fungal culture of the Centre for Ecology and Hydrology Merlewood (UK)
Basidiomycota		
Agrocybe gibberosa (Fr.) Fayod	Saprotroph	Fungal culture of the Centre for Ecology and Hydrology Merlewood (UK)
Amanita muscaria (L. ex Fr.) Hooker	Ectomycorrhiza	Fungal culture of the University of Leipzig (Germany)
Boletus badius (Fr.) Fr.: Fr.	Ectomycorrhiza	Fungal culture of the Centre for Ecology and Hydrology Merlewood (UK)
Laccaria laccata (Scop.: Fr.) Cooke	Ectomycorrhiza	Fungal culture of the University of Leipzig (Germany)
Paxillus involutus (Batsch ex Fr.) Fr.	Ectomycorrhiza	Fungal culture of the University of Leipzig (Germany)
Piloderma croceum Erikss. and Hjorts	Ectomycorrhiza	Fungal culture of the University of Leipzig (Germany)

preferences. There were five replicates per treatment. During the course of the experiment none of the fungal isolates became contaminated with other fungi.

The feeding preferences of oribatid mite species were analysed by single-factor analysis of variance (ANOVA) with the factor "fungi" (ten fungal species). For comparison of means, Tukey's honestly significant difference (HSD) was calculated (Sokal and Rohlf 1995). The food choice (number of faecal pellets) of the respective oribatid mites was analysed by one-way multivariate analysis of variance (MANOVA, Pillai's Trace; Scheiner and Gurevitch 2001) with the factor "fungi" with ten levels (ten fungal species). Subsequently, protected ANOVAs (Scheiner and Gurevitch 2001) were performed to locate which of the oribatid mite species contributed to significant MANOVA results. The analyses were implemented in SAS 8e (SAS Institute Inc., Cary, NC, USA). Data were log-transformed prior to the analysis to increase homogeneity of variance.

Results

Feeding of the oribatid mites significantly differed between fungal species (ANOVA, $F_{9,40}=5.55$; $P<0.0001$). Overall, the ericoid mycorrhizal fungus *Hymenoscyphus*, the ectomycorrhizal fungus *Boletus* and the saprotrophic fungus *Alternaria* were most preferred (Fig. 1a). The ectomycorrhizal fungi *Laccaria*, *Cenococcum*, *Piloderma* and the saprotrophic fungus *Mortierella* were of intermediate preference, whereas *Agrocybe*, *Amanita* and *Paxillus* were less preferred.

Feeding preferences of oribatid mites significantly differed between species (MANOVA, $F_{27,120}=3.61$, $P<0.0001$). *O. tibialis* showed the strongest feeding preferences ($F_{9,40}=8.74$, $P<0.0001$). This species mainly fed on *Hymenoscyphus* and *Alternaria*, little on *Boletus* and *Mortierella* and rejected the other six fungi (Fig. 1b). *N. silvestris* also preferred *Hymenoscyphus* but rejected *Agrocybe*, *Amanita* and *Boletus* ($F_{9,40}=5.74$, $P<0.0001$; Fig. 1c). *C. femoralis* preferred

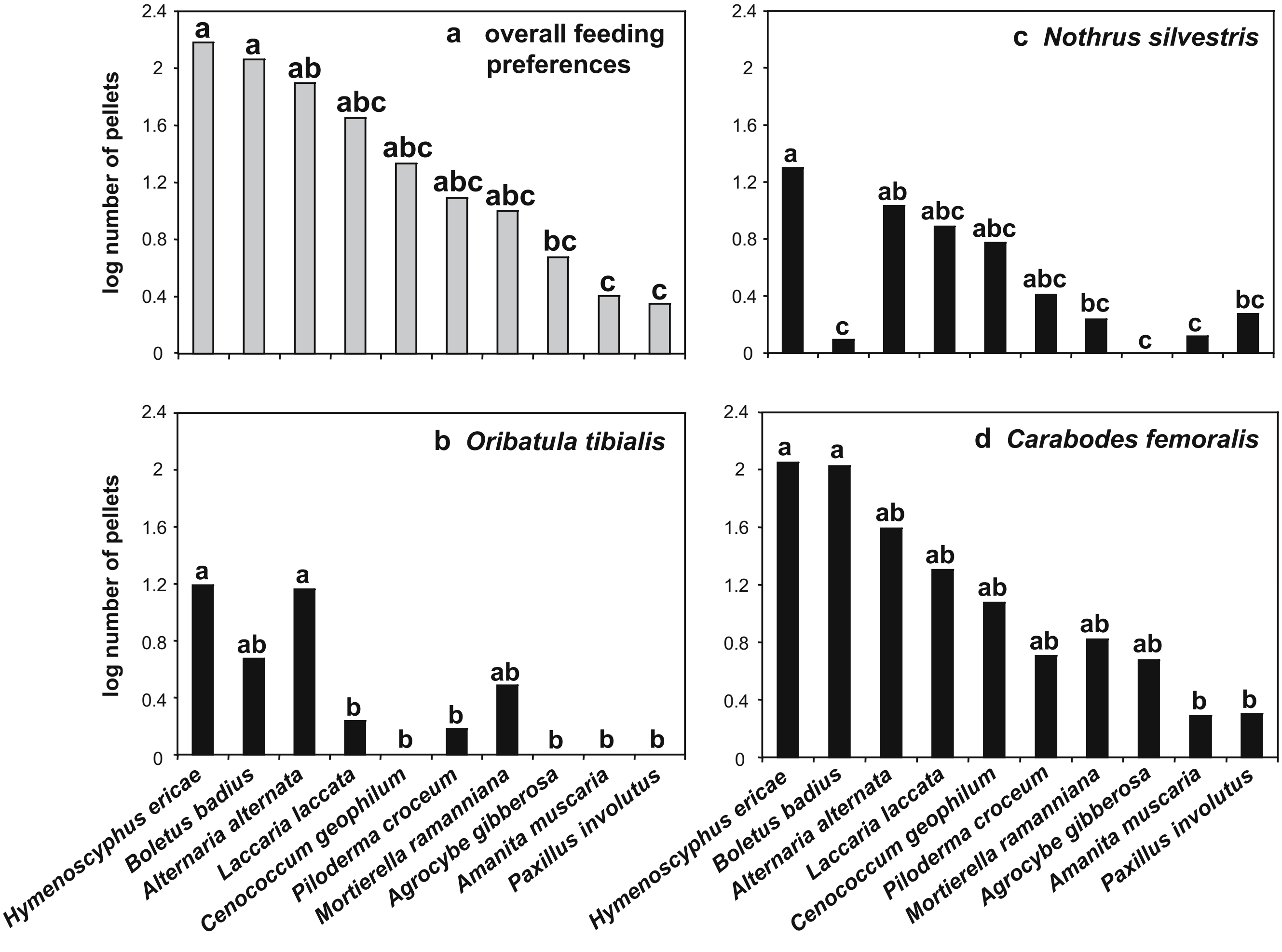

Fig. 1 Feeding preferences (number of faecal pellets) of all oribatid mite species (**a**) of *Oribatula tibialis* (**b**), *Nothrus silvestris* (**c**) and *Carabodes femoralis* (**d**) among six ectomycorrhizal fungi (*Amanita muscaria*, *Boletus badius*, *Cenococcum geophilum*, *Laccaria laccata*, *Paxillus involutus* and *Piloderma croceum*), one ericoid mycorrhizal fungus (*Hymenoscyphus ericae*) and three saprotrophic fungi (*Agrocybe gibberosa*, *Alternaria alternata* and *Mortierella ramanniana*). Fungi were offered simultaneously. Log-transformed data—*bars with different letters* are significantly different

Hymenoscyphus and *Boletus* and also moderately fed on most of the other fungi, but only fed little on *Amanita* and *Paxillus* (Fig. 1d). This species had the broadest feeding range ($F_{9,40}$=3.64, P=0.0021).

Discussion

Differentiation of trophic niches has been suggested to partially explain the coexistence of the high number of soil animal species (Anderson 1975). However, studies on niche differentiation in oribatid mites yielded contradictory results. Some studies concluded that oribatid mites have a wide feeding range (Schuster 1956; Behan-Pelletier and Hill 1983; Scheu and Setälä 2002), whereas others found that oribatid mites generally prefer species of dark pigmented fungi ("Dematiacea") (Mitchell and Parkinson 1976; Maraun et al. 1998, 2003). Furthermore, it has been shown that the feeding preferences of oribatid mite species are different among species of "Dematiacea" (Schneider and Maraun 2005). In addition, stable isotope analyses (^{15}N) of oribatid mite species of four forests indicated that different oribatid mite species occupy different trophic niches (Schneider et al. 2004). In the present study, we investigated ectomycorrhizal fungi as potential food resources for oribatid mites and compared the feeding on these fungi with that on saprotrophic fungi.

Feeding preferences significantly differed between the three oribatid mite species, but overall, all species preferred *Hymenoscyphus*, *Boletus* and *Alternaria*. *Alternaria* ("Dematiacea") is known to be preferred by most oribatid mite species (Hartenstein 1962; Luxton 1966; Schneider and Maraun 2005). Additionally, Ruess et al. (2000) documented that cultures of the fungal feeding nematode *Aphelenchoides* sp. can easily be established on mycorrhizal fungi such as *Hymenoscyphus*. Studies on the interaction between nematodes and mycorrhizal fungi support these results (Giannakis and Sanders 1989; Ruess and Dighton 1996). Only one study investigated the feeding of mycophagous Collembola on ectomycorrhizal fungi (Hiol Hiol et al. 1994) and showed that *P. minuta* preferentially feeds on ectomycorrhizal fungi such as *L. laccata* and *Suillus luteus* (L.) Gray. *L. laccata* was of intermediate preference in our study. Presumably, micro-arthropods prefer fungi (*Hymenoscyphus* and *Alternaria*), suggesting that they are high-quality food. High food quality commonly refers to high nutrient concentrations in food material. Beside nutritional aspects, the morphology and physiology of fungal species can also be critical for the feeding preferences of micro-arthropods. Fungi, such as *Mortierella*, are known to be chitinolytic (Dix and Webster 1995), and oribatid mites are captured in the long hyphae of these fungi. Oribatid mites therefore likely avoid fast-growing fungal species with long hyphae and also toxic species even if the nutrient value of that fungus is high. Fungal species with short hyphae, e.g. *Alternaria* and *Hymenoscyphus*, are likely ingested. Mills and Sinha (1971) concluded that the morphology of mycelia is an important factor for the collembolan *Hypogastrura tullbergi*, which had higher reproduction rates on fungi with low spore count and a mycelia mat that allowed free movement, than on fungi with a thick layer of powdery spores and a dense mycelia mat.

In addition to the ectomycorrhizal fungi, we also offered three saprotrophic fungi as potential food resource for oribatid mites to estimate the quality of the ectomycorrhizal fungi. These three saprotrophic fungi were of different food quality as indicated from former food choice experiments (Ruess et al. 2000; Maraun et al. 2003; Schneider and Maraun 2005). Some mycorrhizal fungi were even as intensively consumed as the high-quality saprotrophic fungus *Alternaria*, suggesting that the feeding of oribatid mites on mycorrhizal fungi is likely important in the field.

In contrast to the results of the food choice experiment of Schneider and Maraun (2005), *O. tibialis* showed strong feeding preferences in this study. *N. silvestris*, also ascribed to unspecialized species (Maraun et al. 1998; Schneider and Maraun 2005), clearly selected certain ectomycorrhizal fungal species. Additionally, the selective feeding of *Carabodes* (Schneider and Maraun 2005) was not supported by results of this study. We suggest that oribatid mites that mainly feed on fungi form two feeding guilds. Some oribatid mite species prefer mycorrhizal fungi, whereas others prefer saprotrophic fungi. Moreover, oribatid mites of both feeding guilds selectively feed on different fungi within the respective group (saprotrophic or mycorrhiza), but in case of shortage of the preferred food, they are also able to feed on other fungi. The lack of a narrow specialisation of oribatid mites may be the consequence of fluctuating availability of the preferred food in the field. Nevertheless, results of this experiment suggest that trophic niche differentiation, at least in part, contributes to the high number of oribatid mites in soil since feeding on mycorrhizal fungi increases the niche space by at least one dimension.

The effects of micro-arthropod grazing on ectomycorrhizal fungi have hardly been studied (but see Hiol Hiol et al. 1994). There is a need for further studies investigating the influence of oribatid mites on ectomycorrhizal fungi since feeding on ectomycorrhizal fungi may affect fungal biomass and changes in fungal community structure, which may have far-reaching consequences for decomposition rates, nutrient cycling and plant growth, as has been shown for collembolan grazing on vesicular–arbuscular (VA) mycorrhizal fungi (Warnock et al. 1982; Finlay 1985; Harris and Boerner 1990; Gange and Brown 1992).

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