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Fungi and Nematoda on *Centromerus sylvaticus* (Araneae, Linyphiidae)

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Summary

More than 30,000 Dutch dune spiders have been checked for the presence of attached organisms: small fungi proved to be the commonest, nematodes were also common. These fungi and nematodes were more or less restricted to spiders of the more vegetated parts of the dunes, and were especially common on winter-adult, litter-inhabiting Linyphiidae. Phenology of this phenomenon and spider body parts involved have been studied in detail for *Centromerus sylvaticus* (Blackwall)—2615 specimens were examined. Fungi appear in the autumn as tiny spots, often on the legs, and develop into more numerous small "brushes" in winter. Fungal infestation rates in *C. sylvaticus* rise from about 20% in November to about 50% in March and later in the last females of the season. Fungi are common on both sexes, whereas nematodes are much more frequent on the active, wandering males. The nematodes are almost always so-called immature "Dauer larvae" of *Rhabditophanes* sp. (Rhabditida). The fungi are non-sporulating and unidentifiable Hyphomycetes. The Nematoda show phoresy. The fungi may involve a mild parasitism. Fungal parasitism of spiders is well known from the humid tropics. Its regular occurrence in temperate Europe seems poorly documented.

Introduction

From 1953 onwards, biologists from the University of Leiden carried out an integrated survey in the Meijendel dunes to monitor the changes brought about by the start of water irrigation in the dunes in November 1955. Part of this survey was a sampling programme for mobile soil fauna using 100 pitfall traps emptied every week, which lasted for seven years (1953–1960). Catches were preserved in 70% alcohol. All large animal groups were identified some time ago, including Lycosidae and Pisauridae (Van der Aart, 1973), and most Gnaphosidae. The remaining spiders were the only major group still unidentified until the first author recently undertook their identification. At the same time, regenerated legs and attached organisms were recorded; many measurements were also taken. for example in order to clarify the phenologies of different species (Noordam, 1996).

Small numbers of exoparasites (pimpline Ichneumonidae) and mites were present on the spiders, but by far the commonest attached organisms were fungi, followed by nematodes. These fungi and nematodes are so tiny that they were overlooked in the beginning, because of the large amount of plant debris, soil particles, etc., adhering to the spiders. Because it is rather time consuming to check a spider for the presence of these fungi and nematodes, only one common species, *Centromerus sylvaticus* (Blackwall), was studied in detail: 2615 specimens were examined. Nearly always only a small number of nematodes (usually 1–5, maximum 20), or fungal spots (usually 1–10, maximum about 50), were present on a spider. The list of spider species given below carrying fungi or Nematoda (Table 1) is only qualitative and undoubtedly incomplete.

	Fungi	Nematoda
Liocranidae		
Agroeca proxima		×
Salticidae		
Heliophanus flavipes		×
Lycosidae		
Trochosa terricola	×	
Theridiidae		
Enoplognatha thoracica		×
Robertus lividus		×
Tetragnathidae		
Pachygnatha degeeri	×	×
Linyphiidae, Erigoninae		
Ceratinopsis romana	×	
Cnephalocotes obscurus		×
Gonatium rubens		×
Leptothrix hardyi		×
Walckenaeria acuminata		×
Walckenaeria antica	×	
Walckenaeria monoceros	×	
Walckenaeria obtusa		×
Linyphiidae, Linyphiinae		
Centromerita concinna	×	×
Centromerus aequalis		×
Centromerus incilium		×
Centromerus prudens	×	×
Centromerus sylvaticus	×	×
Lepthyphantes pallidus	×	×
Neriene clathrata		×

Table 1: Spider species with observed fungi and nematodes, Meijendel dunes, 1953–1960.

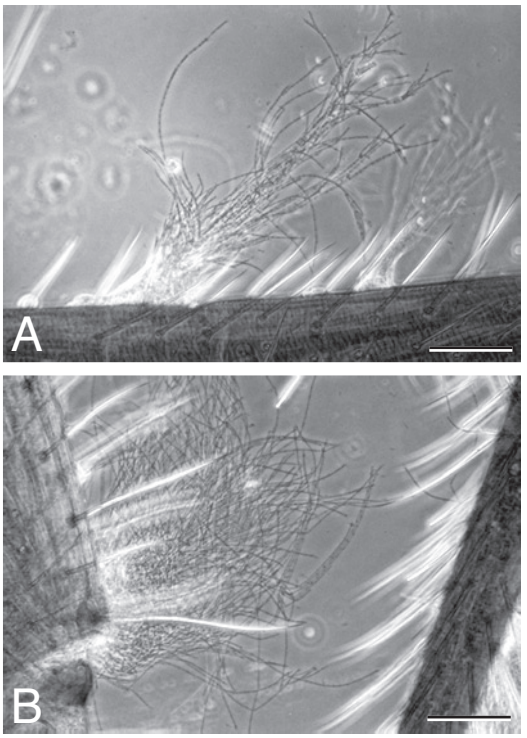

Fig. 1: Fungus on legs of *Centromerus sylvaticus*. Scale lines = 0.1 mm.

For identification of nematodes, material that has been fixed in formaldehyde is essential; material which has previously been preserved in other solutions, such as alcohol, is not suitable. For this reason additional material was collected in the same dunes in November 1994 by means of pitfall traps with 4% formaldehyde as preservative. These fixed nematodes were studied by the third author.

Habitat

Carriers of fungi or nematodes were commonest in thick litter layers, particularly in shade. In thickets with a tree coverage of at least 65%, 35% of *C. sylvaticus* on a whole-year basis carried fungi and 53% of the males carried nematodes. Highest numbers of both fungi and nematodes were present in an aspen (*Populus tremula*) thicket with abundant hop (*Humulus lupulus*, coverage in summer 70%) and a herb layer (coverage in summer 60%) of mainly *Glechoma hederacea* and *Urtica dioica*. Carriers were scarce, but not completely absent, on sandy lichen or marram (*Ammophila*) vegetation; they possibly originated from more vegetated places nearby.

Phenology

Fungal infections are first visible as a few tiny spots, usually on the legs, at the very end of October. They develop to more numerous small brushes (Fig. 1) over the following months. The observed percentage of *C. sylvaticus* with fungi rose from 20% in November to 50% by the end of December and later, and was always somewhat higher in males than in females. Adult males are largely restricted to November and December; adult females can be found until the following summer (Fig. 2). The last females of

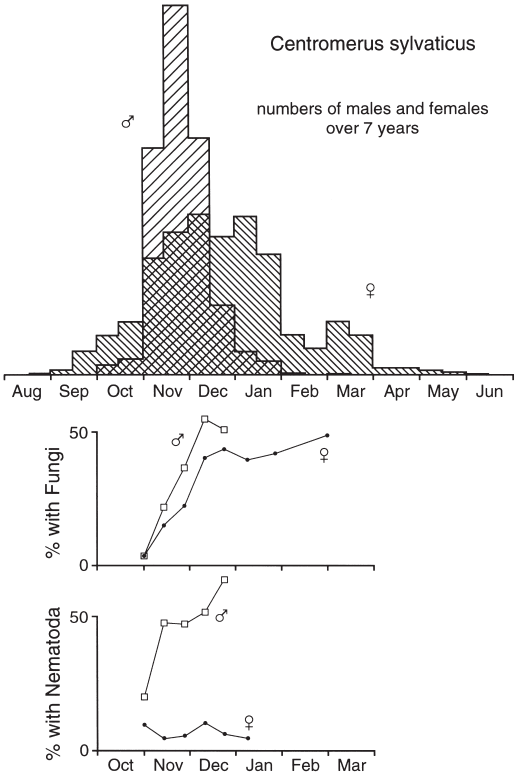

Fig. 2: Phenology of adult *Centromerus sylvaticus* and percentage of this species with observed fungi or nematodes. Total numbers of adult *C. sylvaticus* over seven years: 1211 males, 1404 females.

the season often had their abdomens covered with numerous fungal brushes.

Females rarely carried nematodes (Fig. 2); in males nematode carriers rose from about 20% to about 50% by the end of December.

Body parts involved

Fungal infections were most common on the legs, but could also be found on other parts of the body. In the oldest females, the whole abdomen was often covered with fungal brushes. Often, neighbouring body parts were infected: for example, if the fungus was present retrolaterally on left tibia I, then it also occurred prolaterally on left tibia II. When only one fungal spot was visible, this was more often prolateral on the legs, in males more often dorsal than ventral, but not so in females.

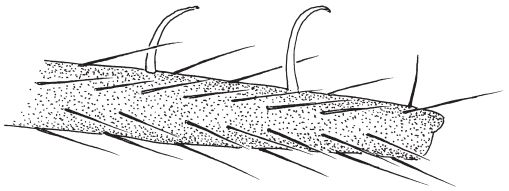

Fig. 3: Dauer larvae (white "spikes") of the nematode *Rhabditophanes* sp. on a metatarsus of *Centromerus sylvaticus*.

Nematodes could be present on every body part, but were most common on the distal parts of the legs (Fig. 3) and pedipalps.

Discussion

Fungi

Fungal parasites have been described from numerous invertebrate hosts. Samson *et al.* (1988) gave an overview of those that are lethal. Workers on Carabidae (Coleoptera) are, for example, familiar with the non-lethal Laboulbeniales (Scheloske, 1969). Lethal fungi on spiders are well known from the tropics (*Gibellula*, *Nomuraea*: Evans & Samson, 1987). In temperate Europe there are a few records of spider specimens with an attached fungus (e.g. Petch, 1948; Nellist, 1965), but the regular occurrence of fungi on spiders is only documented from a few humid places. Bristowe (1958) mentioned two localities with extensive fungal parasitism on spiders: on Jan Mayen Island a species of *Cordiceps* was frequent on (dead) specimens of the four (linyphiid) spider species; in Wheatfen *Torrubiella albolanata* was frequent on linyphiids and on *Antistea elegans*.. Braun (1931) and Crome (1951) described frequent fungal infection of the water spider (*Argyroneta aquatica*) in Germany, where the fungus is usually lethal. The environment of the Dutch dunes is less humid than either of these places. The development of the fungi on *C. sylvaticus* seems to be a slow process. The most virulent entomopathogenic fungi have a rapid development, 10–20 days between infection and sporulation being characteristic, but also four days only have been recorded for fungi on Diptera in the USA (Hutchinson, 1962, cited in Samson *et al.*, 1988). Such virulent fungi can

sometimes wipe out certain insect populations in a short time. The fungi on *C. sylvaticus* could not be identified because they did not sporulate; they grow slowly and very rarely cover a large part of the spider. Therefore, it seems to represent a mild parasitism. But their biology remains unknown; possibly they are essentially saprophytes, with a facultative parasitism on litter-inhabiting invertebrates. It is also possible that they have a host change in spring and autumn. At the least, this large-scale occurrence on *C. sylvaticus* and other winter-active Linyphiidae seems to point to a certain susceptibility to fungal infections. These spiders need a humid environment, but fungal infections perhaps exert selection pressures that keep them out of the wettest microhabitats. For example, under logs where a humidity gradient is present, spiders are rarely found at the most humid end, where Isopoda abound. Brooding geophilomorph centipede females, which live in humid litter or decaying timber, have been observed "mouthing" their eggs. When the female is removed from her eggs, they soon become infected with fungus (Eason, 1964: 40), as if a fungicidal substance is involved in this mouthing. Perhaps (most) spiders are less well equipped in the struggle against fungi. Evans & Samson (1987) mentioned the non-sclerotized abdominal integument of spiders as a factor in this possibly weaker defence. The frequent fungal infection of the water spider *Argyroneta aquatica* is in line with such a greater susceptibility to fungal attack. *Argyroneta* cannot choose a less humid situation for its retreat! Infection of *Argyroneta* by fungi disturbs the hair pattern, which is essential for the air layer around its body (Braun, 1931). According to Crome (1951) fungal infection is responsible for about 90% of the mortality among non-predated water spiders. The impact of fungi on populations of *C. sylvaticus* and other species is unknown but may not be as extreme as on *Argyroneta*. The high percentage (50%) of infected females in habitats which cannot be said to be very humid justifies further study. The male *C. sylvaticus* could be a vector in the transmission of the fungus. The somewhat higher percentage of males with fungi and the distribution of fungi over the body parts are not inconsistent with such a role for the male.

This paper deals only with the results of pitfall trapping, which only catches living organisms. It is possible that an essential part of the life cycle of the fungus has been missed in this way: in other invertebrates sporulation is often observed to occur only when the host dies. Spiders carrying fungi could be placed in a humid box after their death to induce sporulation, thereby facilitating identification of the fungus (Gams *et al.*, 1987).

Nematoda

In contrast to fungi, the nematodes were nearly exclusive to the males of *C. sylvaticus* (Fig. 2), which are active wanderers, and therefore more likely to encounter them than the more sedentary females. The nematodes are phoretic. Only twice has a large parasitic mermithid nematode (Poinar, 1987) been observed from about 50,000 dune spiders. The phoretic nematodes (Fig. 3) are immature, so-called "Dauer larvae", that are sufficiently characteristic to be identified as a species of *Rhabditophanes* (Rhabditida). They fasten their anterior end very firmly to the exoskeleton by a secretion, and free themselves by moulting when the vector arrives in a favourable environment. Bovien (1937) gave a description of the nematode *Cheilobus quadrilabiatus* attached to staphylinid beetles. Recently, the third author has observed them on pseudoscorpions (*Neobisium*, *Roncus*) from leaf litter, soil and humus from Serbia. In the November 1994 samples they were also present on other mobile litter invertebrates; apparently more commonly on more mobile animals (on 17%, 15 out of 87, of the centipede *Lithobius microps*, as against only on one out of 17 pseudoscorpions *Neobisium muscorum*). Phoresy is widespread in nematodes. Beetles of the genus *Aphodius*, for example, transport nematodes of the genus *Rhabditis* from one dung spot to another. These nematodes are apparently able to discriminate between the beetle larvae, to which they do not attach themselves, and the emerging adult beetles (Poinar, 1983).

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