RESEARCH NOTE/NOTA INVESTIGATIVA

SCAVENGING AND INFECTION OF DIFFERENT HOSTS BY *STEINERNEMA CARPOCAPSAE*

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ABSTRACT

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Entomopathogenic nematodes can act as scavenger organisms and to investigate this phenomenon a range of possible hosts was exposed to *Steinernema carpocapsae*. In some cases, differences between an infected insect and a scavenged one were noticed. For example, when infective juveniles of *S. carpocapsae* were applied to arenas with live or dead locusts (*Shistocerca gregaria*), 97.5 % of the live ones were infected, and the nematodes reproduced throughout the body whereas only 19 % of the dead ones were scavenged and the reproducing nematodes were located only in the head of the insect cadavers. Other organisms such as *Agriotes* sp. were not affected by the nematodes when they were alive but around 28% were scavenged. With the differences found between infected and scavenged insects, it is proposed that some insects can be used as ecological markers for the study of scavenging in nature.

Keywords: Adalia bipunctata, Chrysoperla carnea, ecology, entomopathogenic nematodes*, Galleria mellonella, Schistocerca gregaria, Tenebrio monitor, Tipula sp.*

RESUMEN

San-Blas E., B. Pembroke, and S.R. Gowen. 2012. Carroñerismo e infección de diferentes hospedadores por *Steinernema carpocapsae*. Nematropica 42:123-130.

Los nematodos entomopatógenos pueden actuar como organismos carroñeros; para investigar este fenómeno una variedad de posibles hospederos fueron expuestos a nematodos *Steinernema carpocapsae*. En muchos casos la diferencia entre la cantidad de insectos infectados y aquellos que fueron usados como carroña fue notoria. Por ejemplo, cuando los infectivos juveniles de *Steinernema carpocapsae* fueron aplicados en arenas experimentales donde se encontraban saltamontes vivos o muertos (*Shistocerca gregaria*), 97,5% de los vivos fueron infectados y los nematodos se encontraron a través de todo el cuerpo del insecto; mientras que solo en el 19% de los hospederos muertos fueron invadidos y los nematodos se alojaron en la cabeza de los cadáveres. Otro insecto como el *Agriotes* sp. No fue afectado por los nematodos cuando estuvieron vivos, pero el 28% de estos insectos fue usado como carroña. Estas diferencias entre insectos infectados y usados como carroña por los nematodos, pueden ser usados como marcadores ecológicos para estudiar este fenómeno en la naturaleza.

Palavras-chave: Adalia bipunctata, Chrysoperla carnea, ecología, *Galleria mellonella,* nematodos entomopatógenos, *Schistocerca gregaria, Tenebrio monitor, Tipula sp.*

The soil is the natural environment of entomopathogenic nematodes (EPN) which share this habitat with many other microfauna and flora, including antagonists and other pathogens (Kaya, 2002), natural enemies such as nematode trapping fungi, (Jaffee *et al.*, 1992; Jaffee and Strong, 2005) their potential hosts such as soil-dwelling insects and relationships with other groups including isopods (Poinar and Paff, 1985; Eng *et al.*, 2005; Sicard *et al.*, 2008) and annelids (Campos-Herrera *et al.*, 2006). Despite the large number of possible hosts and the continuing discovery of new EPN species, it is uncommon to detect and quantify natural

epizootics produced by these nematodes (Grewal *et al.*, 1995; Peters, 1996; Hominick and Collins, 1997).

The host range of EPN under laboratory conditions has been shown to be very wide. Poinar (1979) infected more than 200 insect species with *Steinernema carpocapsae*, far more than might be expected under field conditions. Peters (1996) listed 14 insect species which have been found naturally infected by *S. carpocapsae.* Also, under laboratory conditions frog tadpoles have been infected or killed by *S. carpocapsae* and *Heterorhabditis bacteriophora* (Poinar and Thomas, 1988). Occasionally EPN have been have reported to reproduce successfully in other invertebrates for example *S. feltiae, S. carpocapsae* and *H. bacteriophora* in the slugs *Deroceras agreste* and *D. reticulatum* (Jaworska, 1993) but this has never been reported under natural conditions.

When nematodes have been applied to control specific pests in the field, some researchers have measured the effect of high densities of nematodes on non-target insects and arthropods. Georgis *et al.* (1991), found no effect of EPN on non-target arthropods in soil or water in a 2 year experiment. Wang *et al.* (2001) did not note any significant changes in the soil arthropod community. This lack of effect on the arthropod or non-target communities does not mean that a few individuals might not have been affected or conceivably the number of non-target organisms affected could have been overlooked.

The possibility of finding material (insect or other arthropod cadavers) in nature is certainly achievable. For example, adult tipulids emerge from pupae and die after a few days, on occasions, the abundance of adult cadavers in the soil could be high [> 10 individuals $*m^2$ day^{-1} (Coulston, 1962)]. Also, there are insects which spend their whole life below ground or insects with very long juvenile stages such as wireworms (*Agriotes* sp.), the larva of which can live up to 5 years (Parker and Howard, 2001). Extreme examples are cicada species (*Magicicada* sp.) which can live underground for up to 17 years (Dybas and Davis, 1962). All of these soil insects can die from natural causes or even be the leftovers of other predatory organisms. In such conditions, scavenging behavior of the EPN can be promoted and this could explain their long term persistence in the soil.

EPN can scavenge and complete their life cycles in *Galleria mellonella* cadavers and it has been shown that they can be attracted to a dead insect (San-Blas and Gowen, 2008). However, because those experiments were done under laboratory conditions, the natural occurrence of scavenging in nature remains unknown. The objective of this paper was to evaluate differences between infected insects and scavenged ones and use that information to postulate and design methods for detecting scavenging under natural conditions.

Steinernema carpocapsae was cultured in fourth instars larvae of *Galleria mellonella* (Lepidoptera: Pyralidae) (Livefoods Direct Ltd. Sheffield, UK) at 20ºC following the technique of Dutky *et al.* (1964). The infective juveniles were collected using a modified White trap (White, 1927) and were stored at 10ºC until the day of the experiment.

Experimental: Two 9 cm Petri dishes were set with a filter paper (Whatman® Nº 1) and 2000 *Steinernema carpocapsae* each. Then 10 dead (killed by freezing -7°C overnight) or live organisms (Table 1) were placed in the dishes. Five days later they were dissected to confirm infection (in the case of originally live specimens) or colonization (in case of originally dead specimens). The only exception was the adult crane flies *Tipula* sp. in which only dead specimens were tested. A set of control dishes (organisms + 1 ml of distilled water) was done to evaluate natural mortality. The experiment was repeated 10 times. The percentages of the hosts in which nematodes were found "scavenging" or "normal" infection in the different treatments were angular transformed and processed with paired t-tests. Differences in angular transformed percentages of "scavenging" and "normal" infection between hosts species were analyzed through ANOVA. When differences were significant, LSD *post hoc* tests were performed. Calculations were done using MINITAB® software. The results were presented without transformation.

The preference of the nematode to scavenge or infect the offered host is shown in Figure 1. Entomopathogenic nematodes scavenged all the insect species which were offered to them. *Steinernma carpocapsae* pattern of preference when scavenging could be separated into 4 groups ($F = 63.3$ $P > 0.001$ $\alpha = 0.05$), the most preferred group is formed by both stages of *G. mellonella* and *Tipula* sp.; while the less scavenged group is represented by *Gryllodes sigilatus*, pillbugs and sowbugs. An interesting element of the results is that the centipede *Lithobius* sp. was scavenged at the same proportion (19 ± 3.2 %) as insects like *Agriotes* sp., *Shistocerca gregaria*, and *Acheta domesticus* and even was higher than *G. sigilatus*.

The "normal" infection also varied on the host species ($F = 81.34$ $P > 0.001$ $\alpha = 0.05$), showing high rates of invasion in almost all insect presented but with less effectiveness on *Gryllus bimaculatus* (33.3 ± 6.32 %) and no infection was reported in *Agriotes* sp. and *Chrysoperla carnea*. Again *Lithobius* sp. was very susceptible to "normal" infection by *S. carpocapsae* (61.25 ± 1.3) and showed a higher rate of infection than *G. bimaculatus*.

The results of the colonization vs. infection of different organisms by *S. carpocapsae* were variable and are summarized in the Table 2. In general, the percentage of scavenging was lower than the percentage of "normal" infection. However, only in 3 insects and the 2 isopods was the relation the opposite. Among insects, in black crickets *G. bimaculatus*, the rate of scavenging doubled the percentage of "normal" infection. When *S. carpocapsae* were scavenging, they were located only in the thoracic section of the crickets, but when they

Table 1. Organisms offered live or dead to *Steinernema carpocapsae*.

Common name	Scientific name	Class: Order	Stage	Source
Silent crickets	*Acheta domesticus*	Insecta: Orthoptera	Nymphs	Livefoods Direct Ltd. Sheffield. UK
Ladybirds	*Adalia bipunctata*	Insecta: Coleoptera	Adults	Syngenta Bioline, Essex. UK
Wireworms	*Agriotes sp.*	Insecta: Coleoptera	Larvae	University of Reading campus
Lacewings	*Chrysoperla carnea*	Insecta: Neuroptera	Larvae	Syngenta Bioline, Essex. UK
Waxworms	*Galleria mellonella*	Insecta: Lepidoptera	Adults/Larvae	Livefoods Direct Ltd. Sheffield. UK
Banded crickets	*Gryllodes sigillatus*	Insecta: Orthoptera	Nymphs	Livefoods Direct Ltd. Sheffield. UK
Black crickets	*Gryllus bimaculatus*	Insecta: Orthoptera	Nymphs	Livefoods Direct Ltd. Sheffield. UK
Locusts	*Schistocerca gregaria*	Insecta: Orthoptera	Nymphs	Livefoods Direct Ltd. Sheffield. UK
Mealworms	*Tenebrio molitor*	Insecta: Coleoptera	Adults/Larvae	Livefoods Direct Ltd. Sheffield. UK
Leatherjackets *	*Tipula* sp.	Insecta: Diptera	Adults/Larvae	University of Reading campus
Earthworms	*Eisenia* sp.	Clitellata: Haplotaxida	Adults and pieces	University of Reading campus
Slugs	*Deroceras* sp.	Gastropoda: Clade Hetrobrabchia	Adults and pieces	University of Reading campus
Snails	*Helix* sp.	Gastropoda: Clade Hetrobrabchia	Adults and pieces	University of Reading campus
Centipedes	*Lithobius* sp.	CChilopoda: Lithobiomorpha	Adults	University of Reading campus
Pill bugs	Unidentified	Malacostraca: Isopoda	Adults	University of Reading campus
Sow bugs	Unidentified	Malacostraca: Isopoda	Adults	University of Reading campus

* Only dead individuals were offered.

Table 2. Percentages of infection and colonization of *Steinernema carpocapsae* in different hosts.

Host	Stage	% of infection	% of colonization	Statistical results
Acheta domesticus	Nymphs	68.57a ± 4.04a	32.86 ± 3.6b	T = -6.0; P < 0.001; d.f.= 18
Adalia bipunctata	Adults	80.15 ± 5.14a	36.31 ± 1.93b	T = -7.97; P < 0.01; d.f.= 18
Agriotes sp.	Larvae	nd	27.88 ± 2.88a	Nc
Chrysoperla carnea	Larvae	nd	21.8 ± 1.98a	Nc
Galleria mellonella	Larvae	100 ± 0a	100 ± 0a	Nc
	Adults	100 ± 0a	94.44 ± 5.56a	T = -1.64; P = 0.199; d.f.= 18
Gryllodes sigillatus	Nymphs	86 ± 2.45a	4 ± 2.44b	T = -12.35; P < 0.001; d.f.= 18
Gryllus bimaculatus	Nymphs	33.3 ± 6.32b	78.3 ± 4.58a	T = 4.30; P < 0.001; d.f.= 18
Schistocerca gregaria	Nymphs	97.5 ± 1.64a	19.0 ± 4.82b	T = -12.92; P < 0.001; d.f.= 18
Tenebrio molitor	Larvae	95 ± 5a	46.47 ± 6.4b	T = -6.59; P = 0.007; d.f.= 18
	Adults	96.76 ± 3.3a	56.6 ± 8.02b	T = -5.55; P < 0.001; d.f.= 18
Tipula sp.	Larvae	98.4 ± 3.2a	95 ± 4.6a	T = -1.62; P = 0.133; d.f.= 18
	Adults	nm	97.6 ± 1.3	Nc
Eisenia sp.	Adults	nd	Nd	-
	Pieces	nm	100	Nc
Helix sp.	Adults	nd	Nd	-
	Pieces	nd	Nd	-
Deroceras sp.	Adults	nd	Nd	-
	Pieces	nd	Nd	-
Lithobius sp.	Adults	61.25 ± 1.3a	19 ± 3.2b	T = -18.06; P < 0.001; d.f.= 18
Pillbugs (Unidentified)	Adults	nd	11.5 ± 6.68a	Nc
Sowbugs (Unidentified)	Adults	nd	3.73 ± 2.74a	Nc

* Different letters within rows mean significant differences α= 0.05. Values are presented as mean ± s.e.m. nd = not detected, nm= not measured nc = not calculated

were infecting, their presence occurred throughout the body. The wireworms *Agriotes* sp. and the lacewing *C. carnea* were unaffected by *S. carpocapsae* but 27.9 ± 2.9 of dead larvae were scavenged. The aspect of the scavenged wireworms was quite similar to the infected *Tenebrio* (brown-yellow color) and the nematodes were found along the body. On the other hand only few nematodes were observed scavenging in *C. carnea* (possibly due to their size) and were located at the head of the cadavers.

It is clear that this behavior might be adopted whenever the opportunity is present. Ecologically, scavenging might represent an important means of long term survival, but contingents upon the recentness and cause of death. The fact that the nematodes can reproduce using dead material as a substrate, in terms of biological adaptation and survival it can be seen as a success.

As previously reported, *G. mellonella* were scavenged as readily as they were infected (San-Blas and Gowen, 2008), adults were also infected and scavenged. Also, both stages of *Tenebrio molitor*, another insect commonly used to test EPN (Brown *et al.*, 2006; Christen *et al.*, 2007), were infected at high rates but the percentages of scavenging were lower, although development of nematodes and the production of IJ seemed to be normal.

In the case of tipulids, there were no differences in the infection or scavenging of the larval stage, in fact the percentages were among the higher of the trial, tipulid larvae can grow up to 4 cm and could be a good food resource for the nematodes. In fact, almost all the dead adults offered to the nematodes were used and the production of offspring was copious. We did not test the infection rates of live tipulids because of their size and fragility and because adults do not naturally spend much time in soil. The cadavers of this insect can represent a major food reservoir for the nematodes after the mating period. The relationship between the mortality of adults (after mating) and the survival of EPN has yet to be tested under natural conditions.

The percentage of infection of *A. domesticus* by *S. carpocapsae* was similar to that reported by Wang *et al.* (1994). Apparently *S. carpocapsae* can avoid encapsulation by the insect immune system (Li *et al.*, 2007). The infection of the locust *S. gregaria* was similar to that reported also by van Sambeek and Wiesner (1999) using *S. feltiae* and *H. megidis.* The infection pattern resembled those found in *G. mellonella* with the characteristic colour, rate of infection, copious production of IJ and in everywhere in the insect body. However, scavenging was considerably lower and nematodes were located only in the head of the cadavers at relatively low levels. The general trend with the orthopterans tested was relatively low percentages of scavenging and high percentages of infections (excepting *G. bimaculatus*). It is possible that decomposition could be quicker than in other insects or there is production of toxic or repellent compounds to EPN.

The abdominal portions of the othopterans contain more material (flesh), than the rest of their bodies, but nematodes seem not be able to access it and remained limited to the head or thorax depending on the offered species. This could suggest that *S. carpocapsae* generally uses the mouth of the insect in the penetration processes (Cui *et al.*, 1993). Nguyen and Smart (1991a) found low percentages of penetration in the abdomen of the orthopteran, *Scapteriscus acletus* by *S. scapterisci.* It is possible that after the insects' death the surviving digestive micro-flora could invade the abdominal zone and compete against the nematodes' symbiotic bacteria.

The ladybird *Adalia bipunctata* was found to be very susceptible to *S. carpocapsae* with infection percentages over 80%. Other species of ladybirds have been tested with similarly high mortality levels (Shapiro-Ilan and Cottrell, 2005). This result probably cannot be extrapolated to field conditions because ladybirds pass more time on the foliage than in the soil. However, the results of the scavenging tests suggest that a proportion of the cadavers could be scavenged by the nematodes after they fall to the soil.

In most cases, there was no diagnostic way to distinguish whether an EPN-infested cadaver recovered from the soil resulted from a scavenging versus a live infection act. In few cases, the general susceptibility trend and infestation specific location could be used in ecological studies of scavenging in natural conditions. For example, there are some hosts that are likely to be scavenged, e.g., the wireworms (*Agriotes* sp.) which were demonstrated as being extremely resistant to infection by *S. carpocapsae* (the same behaviour was also noticed by Půža and Mráček (2010) using *S. kraussei* and *S. affine*). In fact, not a single individual out of 100 was killed by the nematodes, suggesting that they have a very active defense mechanism. The implication of this result is that only EPN-scavenged wireworm larvae would be recovered in the field. Evidently, the effect of other EPN species on live and dead Agriotes has to be tested in order to design methods to measure scavenging in nature.

We found no infections in pill bugs and sow bugs, but a small proportion of them were effectively scavenged; these results differ from Poinar and Paff (1985), who found high percentages of infection in both pill bugs (*Armidillidium* sp.) and especially in sow bugs (*Porcellio* sp.) with *S. carpocapsae* and *Heterorhabditis heliothidis*. The difference between these observations could be related to differences in nematode dosage.

Another interesting finding, concerns the infection and scavenging of the *Lithobius* sp. which are considered as beneficial organisms, preying on (pest) insects. Even though these results cannot be extrapolated to natural conditions, further research may yield more data,

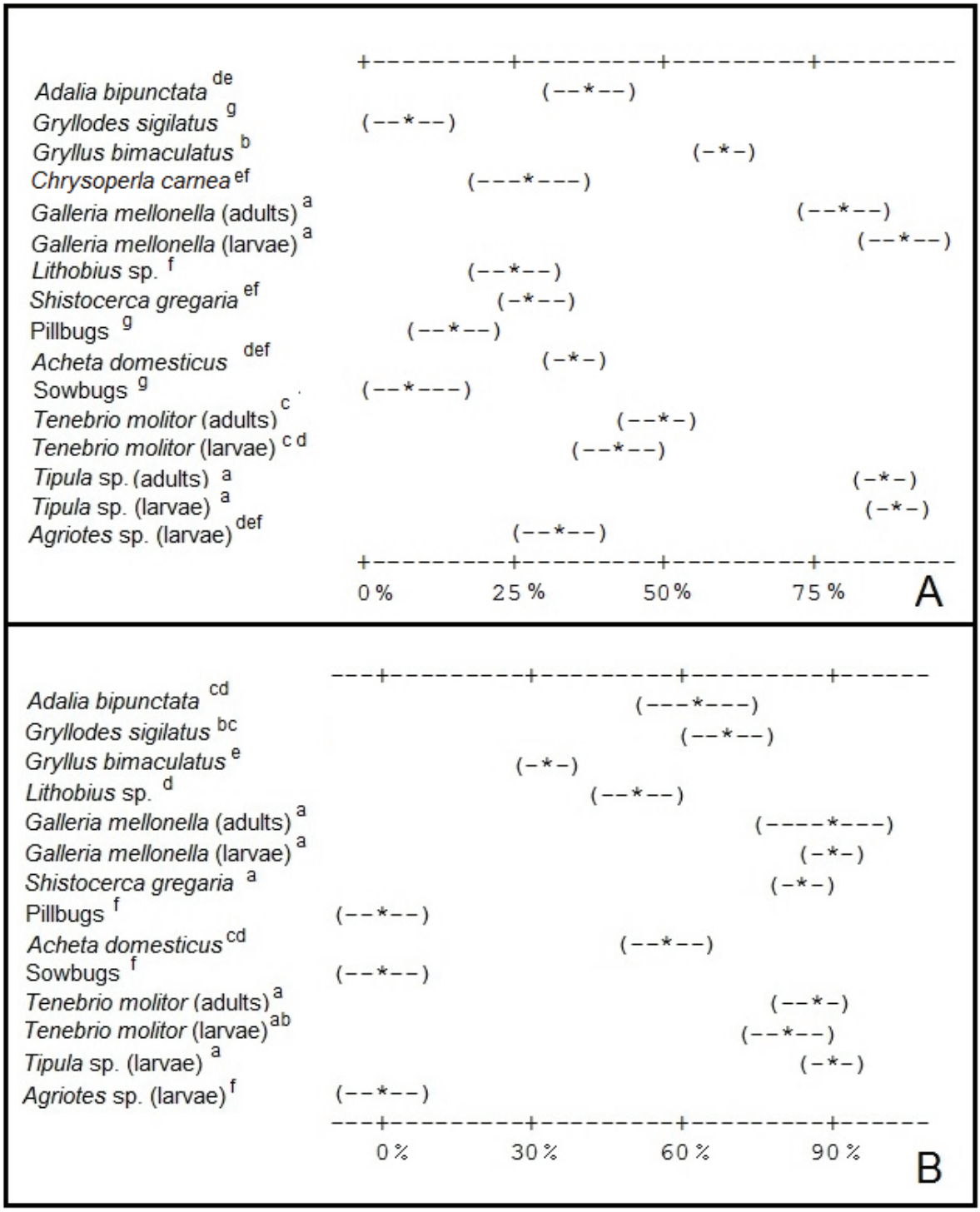

Figure 1: Confidence intervals of percentage of colonization (A) or percentage of infection (B) of *Steinernema carpocapsae* on different organisms. Different letters within rows mean significant differences α= 0.05.

considering that centipedes are soil dwelling organisms and that *S. carpocapsae* has the ability to nictate (Campbell and Gaugler, 1993)

Only pieces of *Eisenia* sp. supported the development and the completion of the EPN life cycle similar results were reported by Capinera *et al.* (1982) who used pieces of *Aporrectodea* sp., and Nguyen and Smart (1991b) who exposed injured and pieces of earthworm (*Allolobophora caliginosa*) to *S. scapterisci.* The two molluscs tested in our experiments, *Deroceras* sp. and *Helix* sp. were neither infected or scavenged by *S. carpocapsae*, these results contrast with those reported by Jaworska (1993), who obtained high infection levels (> 90 %) using *S. carpocapsae* in *Deroceras agreste* and *D. reticulatum*; but not in *Helix pomatia.*

The importance of scavenging of EPN in nature remains to be evaluated, but these results can help as a starting point for the development of sampling techniques and ideas. We demonstrate differences between scavenging and "normal" infection in some of the insects (or even other arthropods). Insects which are scavenged but not infected by EPN or those which present clear differences when they are scavenged can be used as ecological markers for the study of this behavior in nature. These markers can allow us to quantify how important this behavior is for EPN survival and how often they can use this strategy.

We suggest that wireworms (*Agriotes* sp.) could be used to evaluate the frequency of scavenging in the soil as they cannot be killed by *S. carpocapsae* infection. It is conceivable that when insects die in large numbers i.e., when short-lived adult tipulids die after mating, these cadavers would be available for opportunistic scavengers. Knowledge gained by studying a wider host range to establish the site of EPN colonization in different insect hosts will ultimately make it possible to differentiate between insects that have been scavenged or killed by normal infection.

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