RESEARCH NOTE/NOTA INVESTIGATIVA

SCAVENGING AND INFECTION OF DIFFERENT HOSTS BY \textit{STEINERNEMA CARPOCAPSAE}

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\textbf{ABSTRACT}


Entomopathogenic nematodes can act as scavenger organisms and to investigate this phenomenon a range of possible hosts was exposed to \textit{Steinernema carpocapsae}. In some cases, differences between an infected insect and a scavenged one were noticed. For example, when infective juveniles of \textit{S. carpocapsae} were applied to arenas with live or dead locusts (\textit{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 \textit{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.

\textit{Keywords: Adalia bipunctata, Chrysoperla carnea, ecology, entomopathogenic nematodes, Galleria mellonella, Schistocerca gregaria, Tenebrio monitor, Tipula sp.}

\textbf{RESUMEN}


Los nematodos entomopatógenos pueden actuar como organismos carroñeros; para investigar este fenómeno una variedad de posibles hospedadores fueron expuestos a nematodos \textit{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 \textit{Steinernema carpocapsae} fueron aplicados en arenas experimentales donde se encontraban saltamontes vivos o muertos (\textit{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 \textit{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.

\textit{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 \textit{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 \textit{et al.}, 2005; Sicard \textit{et al.}, 2008) and annelids (Campos-Herrera \textit{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 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 20°C following the technique of Dutky et al. (1964). The infective juveniles were collected using a modified White trap (White, 1927) and were stored at 10°C until the day of the experiment.

Experimental: Two 9 cm Petri dishes were set with a filter paper (Whatman® N° 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. Steinernema carpocapsae pattern of preference when scavenging could be separated into 4 groups (F = 63.3 P > 0.001 α = 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 sigillatus, 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 Agrion sp., Heterorhabditis bacteriophora and Acheta domesticus and even was higher than G. sigillatus.

The “normal” infection also varied on the host species (F = 81.34 P > 0.001 α = 0.05), showing high rates of invasion in almost all insect presented but with less effectiveness on Gryllus bimaculatus (33 ± 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*.

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

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

* 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 orthopterans 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 Půzů 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-scallenged 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 (Armadillidium sp.) and especially in sow bugs (Porcellio sp.) with S. carpocapsae and Heterorhabdites 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 $\alpha=0.05$. 

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**A**

- *Adalia bipunctata*  
- *Gryllodes sigilatus*  
- *Gryllus bimaculatus*  
- *Chrysoperla carnea*  
- *Galleria mellonella* (adults)  
- *Galleria mellonella* (larvae)  
- *Lithobius sp.*  
- *Shistocerca gregaria*  
- *Pillbugs*  
- *Acheta domesticus*  
- *Sowbugs*  
- *Tenebrio molitor* (adults)  
- *Tenebrio molitor* (larvae)  
- *Tipula sp.* (adults)  
- *Tipula sp.* (larvae)  
- *Agriotes sp.* (larvae)

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**B**

- *Adalia bipunctata*  
- *Gryllodes sigilatus*  
- *Gryllus bimaculatus*  
- *Lithobius sp.*  
- *Galleria mellonella* (adults)  
- *Galleria mellonella* (larvae)  
- *Shistocerca gregaria*  
- *Pillbugs*  
- *Acheta domesticus*  
- *Sowbugs*  
- *Tenebrio molitor* (adults)  
- *Tenebrio molitor* (larvae)  
- *Tipula sp.* (larvae)  
- *Agriotes sp.* (larvae)

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0%  25%  50%  75%  100%
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 (*Alolobophora 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 agrestis* 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.

**LITERATURE CITED**


