

Interactions between Entomopathogenic Nematodes and Entomophagous Insects

Mohamed Samir Tawfik Abbas

Plant Protection Research Institute, Agricultural Research Centre, Giza, Egypt

Email: samra_mst@hotmail.com

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Abstract

The objective of this review article is to clarify the different interactions between entomopathogenic nematodes, as bio-control agents, against other bio-control agents (parasitoids and predators) proposed by the researchers. Thus, it gives clear information concerning the potential of combining them as a part of Integrated Pest Management (IPM) programs against insect pests. Some laboratory studies showed that the treatment of predacious insects by entomopathogenic nematodes (EPNs) at different concentrations can infect and kill the treated larva, nymphs and adults of predators. The percentages of mortality were found to be high (up to 100%), moderate (15% - 35%) or low (3% - 7%). Other studies revealed the resistant of treated predators to nematode-infection. Some predators that were offered infected prey avoid feeding on such prey and, in contrast, the soil predators (ants and mites) consumed the offered cadavers as well as the infective juvenile of the nematodes and did not show any detrimental effects. Mostly, parasitoids cannot complete their development inside or on nematode-infected hosts if parasitism occurs before or early after infection. The parasitoid females may avoid laying eggs in the infected hosts or cannot discriminate between healthy and infected hosts. A field study demonstrated that applying EPNs combined with the predator, *Labidura riparia* significantly reduced the population of the target pest compared to the nematode or the predator alone. Also, two field experiments indicated that the combination of parasitoids and nematodes can be successful for insect pest management.

Keywords

Entomopathogenic Nematodes, *Steinernema*, *Heterorhabditis*, Parasitoids, Predators, Entomophagous Insects

1. Introduction

Combination of entomopathogens and other biological control agents (parasi-

toids and predators) can be synergistic, additive or antagonistic depending on the specific biological control agents and their rate, timing of application and host species [1]. Synergistic interactions result in a higher mortality than the combined individual mortalities of the pest population. Additive interactions occur if the natural enemies do not interact and, thus, the total level of mortality is equivalent to the combined individual mortalities caused by each agent. The antagonistic interactions occur if the total mortality is less than when either natural enemy acts alone [2].

Entomopathogenic Nematodes (EPNs)

The free-living, non-feeding 3rd stage infective juveniles (IJs) of the entomopathogenic nematodes (EPNs) of the genera *Steinernema* and *Heterorhabditis* in the (families Steinernematidae and Heterorhabditidae, respectively) possess attributes of both insect parasitoids or predators and microbial pathogens. Like parasitoids/predators, they have chemoreceptors and are motile, in soil, looking for suitable host. Like pathogens, they are highly virulent, killing the host quickly and can be cultured easily *in vivo* and *in vitro* [3]. The members of both families are associated with mutualistic bacteria of the genera *Xenorhabdus* (for Steinernematidae) and *Photorhabdus* (for Heterorhabditidae) [4]. IJs can locate the host by detecting the insect excretory products, carbon dioxide levels, temperature gradients and movement of the host. The IJs then penetrate the host through natural openings; mouth, anus or spiracles, and in addition, IJs in heterorhabditids possess a tooth that enables them to penetrate the host through the cuticle of certain insects. Once they enter the hemocoel, they release the bacteria which multiply and kill the host by septicaemia [5]. EPNs have positive characters including their broad host range, safety to vertebrates, plants and non-target organisms [6], exempting from registration in many countries, easily applied using a standard spray equipment [5], compatible with many chemical and bio-pesticides and amenable to genetic selection [7]. In field application, commercially, a dose of 2.5 - 5 × 10⁹ IJs/ha was recommended to give effective control comparable to chemical insecticides [8]. The EPNs have great potential to be used in integrated pest management programs. They are more specific, proven to be safe and effective alternatives to chemical pesticides. The susceptibility of insect pests varies depending on the selectivity and applied rates of EPN species. Location of the host by IJs within the soil is one of the most important factors where their movements are affected by temperature and oxygen levels. Temperature, moisture, aeration and soil type, the species of EPN, age of target insects and soil fauna are important factors affecting the activity of EPNs.

Parasitoids and Predators

Parasitoids and predators are among the biological control agents that play an important role, naturally, against agricultural pests infesting field crops, vegetables, orchards and ornamentals. They constitute a considerable part within IPM programmes which include suitable timing of plantation, suitable agricultural practices, using biological control agents (parasitoids, predators and entomopa-

thogens) and finally selective chemical insecticides if needed [9].

2. Interactions between EPNs and Predators

2.1. Impact of EPNs on Treated Predators

2.1.1. Laboratory Experiments

The nematode, *Steinernema kraussei* did not infect the larvae of 2 dipteran predators of the sawfly, *Cephaleia abietis* (L.): *Thereva handlirschi* Krober (Fam. Therevidae) and *Rhagio notatus* (Meigen) (Fam. Rhagionidae) when treated with a concentration of 5000 IJs/ml in Petri-dishes [10]. At a concentration of 20 IJs/cm² in Petri-dishes, the immature and adult stages of the earwig, *Labidura riparia* Pallas (Dermaptera: Labiduridae) were resistant to infection by *Heterorhabditis bacteriophora* Poinar and *S. carpocapsae* (Weiser) [11]. Also, *S. scaptetris* Nguyen & Smart did not cause mortality in treated European earwig, *Furficula auricularia* (L.) [12]. Also, *Dalotia coriaria* (Kratz) (Col., Staphilinidae), a common predator of the flower thrips, *Frankliniella occidentalis* (Pergande) was not susceptible to *S. feltiae* at concentrations of 12, 25 and 50 IJs/cm² [13]. Similarly, investigating the pathogenicity of 3 commercial nematode species to adults and 3rd instar larvae of *D. coriaria* at 3 concentrations (50, 100 and 200 IJs/cm²) showed that mortality percentages for the 3 nematode species did not differ significantly from the control [14]. Testing the impact of *H. bacteriophora* on eggs, larvae and adults of *Chrysoperla zastrowi sillemi* (Espen. Peterson) sprayed with the nematode suspension containing 5000 IJs (10 eggs or larvae or adults /Petri-dish) showed that the nematode did not affect, significantly, egg-hatching and survival of larvae or adults of the predator. Microscopic examination of the treated eggs, larvae and adults exhibited no morphological or physical changes [15]. Similarly, *S. carpocapsae* did not cause mortality in the 2 mirid predators, *Macrolophus pygmaeus* Rambur and *Nesidiocoris tenuis* Reuter when treated in pots at a concentration of 50 IJs/cm²/5 nymphs or adults [16].

In contrast to the above mentioned studies, the staphylinid predator, *Philonthus* sp. was found to be infected with *H. bacteriophora* and *S. carpocapsae* and the adult was less susceptible than the 3rd larval instar [8]. Also, a high mortality of the coccinellid, *Coccinella undecimpunctata* (L.) was caused by *S. carpocapsae* and *H. taysearae* [17]. The pathogenicity of EPNs, *S. carpocapsae* (Weiser), *S. feltiae* (Filipjev) and *Heterorhabditis bacteriophora* Poinar was evaluated against the aphid predator, *Aphidoletis aphidimyza* (Rondani) (Dipt.: Cecidomyiidae) at 3 concentrations; 100, 1000 and 10,000 IJs/Petri-dish/10 larvae. The results showed that percent mortality in the treated larvae at the 3 tested concentrations ranged 33% - 92% by *S. carpocapsae*, 20% - 78% by *S. feltiae* and 9% - 93% by *H. bacteriophora* [18]. Similarly, the efficacy of 3 species of EPNs was studied against larvae of the coccinellid, *Adalia bipunctata* (L.) and the chrysopid, *Chrysoperla carnea* Steph. at concentrations of 500, 2500 and 5000 IJs/ml/20 larvae. Percent mortality in *A. bipunctata* larvae ranged 84% - 97% by *S. feltiae*, 79.5% - 100% by *S. carpocapsae* and 43.6% - 98% by *H. bacteriophora*. The re-

spective values for *C. carnea* were 42% - 66%, 90% - 100% and 36.5% - 65.8% [19]. At a concentration of 25 IJs/cm² in Petri-dishes, *S. carpocapsae* caused 84.3% mortality in the European earwig, *F. auricularia* 48 h post treatment [20].

2.1.2. Semi-Field and Field Experiments

A field experiment revealed that *S. krausseii* did not cause detrimental effect on the populations of the dipteran predators of the sawfly, *Cephaleia abietis* (L.). The predators were *Thereva handlirschi* and *T. valida* Flekr (Fam. Therevidae) and *Rhagio notatus* and *R. scolopacea* (L.) (Rhagionidae) [10]. Similarly, in a cabbage field experiments, it was found that *S. carpocapsae* and *H. bacteriophora* did not affect the numbers of the earwig, *Labidura riparia* Pallas and other non-target soil arthropods in comparison with the untreated cabbage [11]. The combined releases of the predatory mite, *Hypoaspis culeifer* (Canestrini) (Acari: Laelapidae) and two nematode species, *H. bacteriophora* and *S. feltiae* was evaluated against soil-dwelling stages of the thrips, *Frankliniella occidentalis* (Pergande) in pots [21]. The results indicated that *H. culeifer* reduced the proportion of adult thrips emergence by 46% in comparison with the control. Also, *S. feltiae* and *H. bacteriophora* reduced adult thrips emergence by 46% and 61%, respectively. Significant lower emergence % of adult thrips was obtained by combined treatments with the nematodes and the predatory mite, than individual application of the nematodes or the predator. In a greenhouse experiment, *S. carpocapsae* and *H. bacteriophora* were applied at concentrations of 25 and 250 IJs/cm² of soil (in pots) against aphids treated with 3rd instar larvae of the predator, *Aphidoletis aphidimyza* (Ronden) [18]. *S. carpocapsae* caused 30% and 67% mortality at the 2 concentrations, respectively, in the larvae of the predator, *A. aphidimyza* compared to 49% and 81% mortality by *H. bacteriophora*. The compatibility of soil-dwelling predacious mites with *S. feltiae* at a concentration of 50 IJs/cm² for controlling the thrips, *F. occidentalis* was investigated in pots [22]. The predacious mites were *Stratiolaelaps scimitus* (Womersley) and *Gaeolaelaps gillespiei* Beaulieu (Acari: Laelapidae). The results showed that *S. scimitus* was not significantly affected by *S. feltiae* while *G. gillespiei* was adversely affected (57.5% mortality).

2.2. Discrimination between Healthy and Nematode-Infected Prey

The earwigs were found to have the ability to avoid feeding on nematode-infected prey [23]. Also, the third larval instar and adults of the carabid predator, *Calosoma granulatum* (Coleoptera), avoided feeding on *Spodoptera frugiperda* larvae infected with *H. amazonensis* [24]. When the predator 1st instar larvae had access to the infected cadavers as food, most of them died within 6 days of feeding.

2.3. EPNs as Prey for Predacious Insects and Mites in Soil

The workers of the ant species (Fam. Formecidae): *Linepithema humile* (Mayer), *Veromessor Andrei* (Mayr), *Pheidole vistana* Forel, *Formica pacifica* Francoeur,

and *Monomorium ergatogyna* Wheeler were found to feed on steinernematid-killed insects in soil but did not feed or fed very little on heterorhabditid-killed insects [25]. In addition, when *L. humile* was offered steinernematid-killed insects, it attacked 70% - 80% of such insects compared to 5% - 35% when offered heterorhabditid-killed insects. When 6-day old nematode-killed larvae of *Ceratitis capitata* (Wied) (with emerging IJs) were exposed to the mite, *Sancassania polyphyllae* Oudenmans (Acari: Acaridae), the cadavers were consumed along with 96% of the emerging IJs [26]. The authors suggested that this fact could negatively impact the role of EPNs as biological control agent.

The effects of different soil arthropods on EPNs were studied under laboratory conditions as some predacious insects in soil may consume cadavers of nematode-killed insects [27]. The tested predators were offered *S. feltiae* and *H. bacteriophora* -infected larvae of *Galleria mellonella* (L.). The studies showed that: a. All tested nymphs and adults of the American cockroach, *Periplaneta Americana* (L.) (Fam. Blattidae) and the cricket, *Gryllus bimaculatus* De Geer (Orthoptera: Gryllidae) consumed *Steinernema*- and *Heterorhabditis*-killed *Galleria* larvae one day post infection. 89% and 58% of the 2 tested insects, respectively, consumed the infected larvae at 2-day post-infection. b. *Labidura riparia* adults, however, partly consumed only *Steinernema*-infected larvae at 2-day post-infection. None of the three tested insects consumed the nematode-killed larvae at 3-day post infection. c. The predacious mite, *Sancassania polyphyllae* consumed nematode-killed insects but did not consume free-living IJs in the soil environment. d. The ant, *Tetramorium chekheti* Forel (Hym.: Formicidae) consumed the *S. feltiae*-killed larvae but not those killed by *H. bacteriophora*.

3. Interactions between EPNs and Parasitoids

3.1. Laboratory Experiments

3.1.1. Effect on Developmental Stages of Parasitoids inside Their Hosts

H. indica did not affect percent emergence of *Trichogramma chilonis* and *T. japonicum* Ashmead in treated parasitized eggs of *Corcyra cephalonica* Stainton [28]. The same results were obtained by using *H. bacteriophora* [15].

Larvae of the tachinid parasitoid, *Myxecoristops* sp. did not complete its development in parasitized sawfly, *Cephaleia abietis* (L.) larvae treated with *Steinernema kraussi* [10]. Also, the tachinid parasitoid, *Compsilura concinnata* (Meigen) proved to be susceptible to *N. carpocapsae* and its associated bacterium, *Xenorhabdus nematophilus* [29]. In addition, the death of the braconid larval parasitoid, *Apanteles militaris* Walsh. in its host larvae, *Pseudaletia unipuncta* (Haworth) was observed as a result of the death of its host infected with *Neoplectana carpocapsae* before the parasitoid could complete its development. However, when the parasitized larvae were treated with the nematode late (11 days after parasitism), 94% of the parasitoid larvae emerged from the host and formed normal pupae. The treated cocoons, however, were found to be resistant to nematode infection [30]. In contrast, investigating the pathogenicity of *S.*

scapterisci to larvae and pupae of the tachinid, *Ormia deplete* (Wied.), a parasitoid of the mole cricket, *Scapteriscus vicinus* Scudder (Orth.: Gryllotalpidae) revealed that % emergence of parasitoid adults from treated larvae and pupae did not differ significantly from the control [31].

S. carpocapsae caused high rates of mortality in *Cardiochelis diaphaniae* (Marsh) larvae, a braconid larval parasitoid of the melon worm, *Diaphania halinata* (L.). However, the pupae in their cocoons were resistant to infection [32]. The susceptibility of larvae, pupae and adults of the braconid ecto-larval parasitoid, *Bracon hylobii* Ratz. to *H. downesi* (both are natural enemies of the pine weevil, *Hylobius abietis* (L.)) was tested [33]. When the nematode was applied on the parasitoid larvae feeding on its host larvae, the nematode readily infected such parasitoid larvae and there was a reduction in cocoon formation and fewer cocoons gave rise to adults. When the parasitoid cocoons were treated with the nematode, nearly all emerging adults were killed by the nematode infection. The 3rd instar larvae of *S. littoralis* (parasitized with the braconid, *Microplitis rufiventris* (Kok.)) were treated with *H. bacteriophora* and *S. carpocapsae* (1200 IJs/5 parasitized larva/Petri-dish) harboring the egg stage, mid 1st, 3rd and late 3rd instars of the parasitoid [34]. It was found that the percentages of hosts that gave rise to adult parasitoids after treatment with *S. carpocapsae* were 12, 11, 16 and 53% for egg, mid 1st, 3rd and late 3rd instar of the parasitoid on host larvae, respectively. The respective values for *H. bacteriophora* were 0.0, 0.0, 0.0 and 52%.

The interactions between the nematode, *S. carpocapsae* and 2 ichneuminid ecto-larval parasitoids: *Mastrus ridibundus* (Grav.) and *Liotryphon caudatus* (Ratz.) of the codling moth (CM), *Cydia pomonella* (L.). was investigated [35]. Exposing the middle-aged developing larvae of the parasitoids within *C. pomonella* cocoons to the nematode at a concentration of 10 IJs/cm² in Petri-dishes (10 larvae/dish) resulted in 70.7 and 85.2% mortality in *M. ridibundus* and *L. caudatus*, respectively. However, the diapausing full-grown larvae of both parasitoids were almost completely protected from IJs penetration within their own tight cocoons. Percentage of mortality in adults of *Necremnus artynes* (Walker), an eulophid larval parasitoid of tomato leafminer, *Tuta absoluta* (Mayrick), treated with *S. carpocapsae* (at a concentration of 50 IJs/cm² of a plant leaf containing 5 adults did not differ significantly from untreated adults [16].

3.1.2. Discrimination between Healthy and Nematode-Infected Host

The females of the parasitoid, *Diglyphus begini* Ashmead were unable to discriminate between *S. carpocapsae*-infected and non-infected *Liriomyza trifolii* larvae. [36]. Similarly, the female of the ecto-parasitoid, *Habrobracon hebetor* exposed to larvae of *Plodia interpunctella* infected with *H. indica* together with healthy larvae did not discriminate between the two [37]. In contrast, the female of the braconid ecto-larval parasitoid, *Bracon hylobii* Ratz. did not oviposit on the *H. downesi*-infected pine weevil larvae, *Hylobius abietis* 1 - 7 days before exposing to the parasitoid [33]. Similarly, the females of 2 ichneuminid ecto-larval parasitoids: *Mastrus ridibundus* (Grav.) and *Liotryphon caudatus*

(Ratz.) of the codling moth (CM), *Cydia pomonella* (L.) were able to detect and avoid depositing eggs in *S. carpocapsae*-treated cocooned CM larvae as early as 12 h post treatment. When given the choice between untreated cocooned CM larvae and those treated with nematode (25 IJs/cm², equal to LC₉₅ for CM larvae) 12, 24 and 48 h earlier, the female parasitoids preferred, significantly, the untreated ones [35].

3.1.3. Combined Effect of Parasitoids and EPNs on the Host

A higher percent of mortality occurred in larvae of *Liriomyza trifolii* (Burgess) when the eulophid parasitoid, *Diglyphus begini* Ashmead was released combined with *S. carpocapsae* [36]. In contrast, investigation of the compatibility of larval parasitoids and *S. feltiae* in controlling the leaf-miner, *Liriomyza huidobrensis* (Blanchard) indicated that larvae, in their mines, already parasitized by *Diglyphus isaea* (Walker) or *Dancus sibirica* (Maklin) were found to be infected with *S. feltiae* following a foliar application of the nematode [38]. In addition, tests to investigate the utilization of *D. isaea* following foliar application of the nematode revealed that adult parasitoids did not discriminate between healthy and nematode-infected larvae for feeding [38].

The potential of integrating the application of *H. indica* and releasing the parasitoid, *Habrobracon hebetor* (Say) for the management of the Indian meal moth, *Plodia interpunctella* (Hubner) was studied [37]. It was found that the combination of the nematode and parasitoid increased % mortality of the insect larvae. Release of the parasitoid or application of the nematode (200 IJs/larva) alone caused 62% and 71% mortality, respectively, in *Plodia* larvae whereas combination of both resulted in 99% mortality. The nematode was found to be virulent to the parasitoid larvae but not to pupae or adults. The nematode IJs preferred infecting parasitized larvae compared to non-parasitized ones.

3.2. Field Experiments

In field experiments, the nematodes, *S. carpocapsae* and *H. downesi* did not affect the natural populations of the parasitoid, *Bracon hylobii* developing on *Hylobius abietis* [39]. Similarly, application of *H. bacteriophora* for controlling the Caribbean fruit fly, *Anastrepha suspensa* (Loew) did not affect, significantly, the population densities of *Diachasmimorpha longicaudata* Ashmead, a braconid larval parasitoid of *A. suspensa* [40]. It seems that *H. bacteriophora* could be more promising when combined with *D. longicaudata* for the control of Caribbean fruit fly.

4. Discussions

Direct treatment of predators with EPNs in laboratory revealed that some species were found to be highly susceptible to infection [8] [17] [18] [19] [20] and others showed resistance [10]-[16]. However, the European earwig, *Furficula auricularia*, was found to be resistant to *S. scapterisci* [12] and highly susceptible to *S. carpocapsae* [20]. Also, the staphilinid predator, *Dalotia coriaria* was re-

ported to be resistant to *S. feltiae* [13] [14] while the staphilinid, *Philonthus sp.* was susceptible to *H. bacteriophora* and *S. carpocapsae* [8]. Similarly, *Chryso-perla carnea* proved to be highly susceptible to *S. carpocapsae* and *H. bacteriophora* [19] while *C. zastropfi sillemi* was resistant to *H. bacteriophora* [15]. Laboratory studies revealed that the earwig, *Labidura riparia* was resistant to *S. carpocapsae* and *H. bacteriophora* [11] while in an experiment in a cabbage field both nematodes did not affect its population [11]. On the other hand, predators consume nematode-infected prey, with no negative effects on their biological parameters, and, in addition, soil predators may feed on the free-living infective juveniles. Thus, such predators may negatively reduce the populations of the EPNs in the environment.

Mostly, parasitoids cannot complete their development inside or on nematode-infected hosts if parasitism occurs before or early after infection [10] [29] [30] [32] [33] [34] [35]. However, the tachinid, *Ormia deplete* (Wied.), could develop successfully in its host, the mole cricket, *Scapteriscus vicinus* Scudder (Orth.: Gryllotalpidae) [31]. The parasitoid females may avoid laying eggs in the infected hosts [33] [35] or cannot discriminate between healthy and infected hosts [36] [37]. Two field experiments indicated that the combination of parasitoids and nematodes did not affect, significantly, the populations of the parasitoids [39] [40].

EPNs are applied mainly in the field as bio-control agents against soil-dwelling insects, insects in cryptic habitats, insects pupate in soil as well as insects drop in soil for shade in hot weather (as noticed with *Spodoptera* spp. and the red palm weevil) [41]. Thus, it can be claimed that the combination of EPNs and parasitoids or predators is expected to have a considerable role in IPM programs against insect pests with no probable contact or effect on such natural enemies on the aerial parts of the plants. Further field studies should be done to obtain enough and reliable information concerning this claim.

Conflicts of Interest

The author declares no conflicts of interest regarding the publication of this paper.

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Abbreviations

Entomopathogenic nematodes (EPNs)

Infective juveniles (IJs)