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Curr Biol. Author manuscript; available in PMC 2015 November 28.

Published in final edited form as:

Curr Biol. 2012 June 5; 22(11): R430–R431. doi:10.1016/j.cub.2012.03.047.

Entomopathogenic Nematodes

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What are entomopathogenic nematodes?

Nematodes seem to have evolved to occupy nearly every niche imaginable, including a wide diversity of parasitic niches. Among the vast variety of parasitic nematodes, some have evolved an association with insect pathogenic bacteria. Together the bacteria and nematode are a lethal duo. These nematodes are called 'entomopathogenic nematodes' or EPNs for short. Essentially the nematodes serve as mobile vectors for their insect-pathogenic bacteria cargo, like little Typhoid Marys. The nematodes seek out and invade potential hosts and release their pathogenic payload into the nutrient-rich hemolymph. Infected insect hosts die quickly, the bacteria proliferate, the nematodes feed on bacteria and insect tissues, and reproduce. When the host cadaver is depleted of resources, nematodes associated with pathogenic bacteria emerge and search for new hosts to infect (Figure 1). The cooperation with bacteria and the speed with which they kill sets EPNs apart from other nematode parasites.

How do they kill?

The nematode and the pathogenic bacteria they carry contribute to varying degrees, depending on the combination. The known bacterial associates of EPNs, species of *Photorhabdus* and *Xenorhabdus*, are known to produce a toxic cocktail of secondary metabolites that are not only lethal to the insect hosts, but that prevent opportunistic bacteria and fungi from utilizing the nutrient rich cadaver, sequestering the resources for themselves and their nematode partners. The bacteria always contribute to the virulence of the duo, and usually contribute the lion's share. Some species of nematodes are thought merely to shuttle the bacteria, contributing very little to host death, while others are known to be lethal in their own right, producing a variety of secreted protein products that degrade and digest host tissues, in addition to short-circuiting the host immune system. Even though some nematodes appear lethal on their own, no non-bacterial associated EPNs are known to exist.

Are all stages infectious?

The short answer is no. Only a modified third larval stage called the infective juvenile, analogous to the dauer juvenile stage in *Caenorhabditis elegans*, is infectious. In fact, infective juveniles are the only free-living stage of known EPNs, while all other

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developmental stages are only found inside infected hosts. The infective juvenile is a stress tolerant, non-feeding, bacterial vectoring stage that seeks out insects to infect and kill.

How did they get their name?

The first entomopathogenic nematode was described by Gotthold Steiner in 1923; since then more than 75 species have been described, with more species being described every year. Most studies focus on EPNs from two genera: *Steinernema* and *Heterorhabditis*. It is through their association with insect pathogenic bacteria that they began to be called entomopathogenic nematodes. First the nematodes' bacterial partners were called entomopathogenic bacteria, because these bacteria have a median lethal dose or LD_{50} of ten thousand cells or less. This means that an inoculum of ten thousand bacterial cells or less, into the hemolymph, kills half of a tested population of insects. The term 'entomopathogenic' began to be applied to the nematodes themselves in the late 1980's and reinforces the link between nematology and insect pathology. It is a useful technical epithet that differentiates them other types of parasitic nematodes, of which there are many.

Are they harmful to humans?

While most parasitic nematodes might be seen as harmful, EPNs are beneficial to humans. Their potential as alternatives to chemical pesticides for controlling pesky insects was recognized early on and they have been subjected to extensive laboratory and field-testing. EPNs have been used in biological control since the 1930s and are currently used worldwide. For example, they have been used with high levels of success to control invasive species of mole crickets in Florida and continue to be used in orange groves in both Florida and California to control the citrus root weevil and other damaging crop pests. EPNs are even commercially available for pest control in home gardens and are commonly marketed as 'beneficial nematodes.'

Why are EPNs being studied?

For starters, the symbiotic association with bacteria is highly specific in most cases and provides an excellent model for understanding the development and evolution of symbiosis. EPNs' potential as biological control agents continues to be evaluated with studies focusing on selection of desirable traits such as virulence, heat and stress tolerance, persistence, etc. Because at least two distantly related genera have evolved this specific type of parasitism (*Heterorhabditis* and *Steinernema)*, EPNs are an interesting system for the study of convergent and parallel evolution. Also, since they are odd intermediates between predators and parasitoids, there are many studies regarding their host-seeking behavior. They rely primarily on chemoreception for host seeking and some of them are capable of jumping, which is an extraordinary behavior in nematodes that is unique to some *Steinernema*. Imagine, a 0.5 – 1 mm worm with no legs or hard body parts, and yet it is capable of jumping up to 9 times its body length.

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What remains to be explored?

There is much that remains unknown about EPNs, including: their global abundance and diversity, the extent of their host range and whether or not other arthropods or even non-arthropods are also infected, what has led to the specialization of some for certain hosts and not others, what drives niche partitioning within this guild, the molecular underpinnings of their symbiosis and parasitism, how they can survive carrying highly pathogenic bacteria, how they suppress or avoid host immunity, or just how genetically similar disparate species that have converged on this very particular lifestyle are. These and other questions remain underexplored, providing plenty of room for studying these fascinating, useful, and delightful worms.

Where can I find out more?

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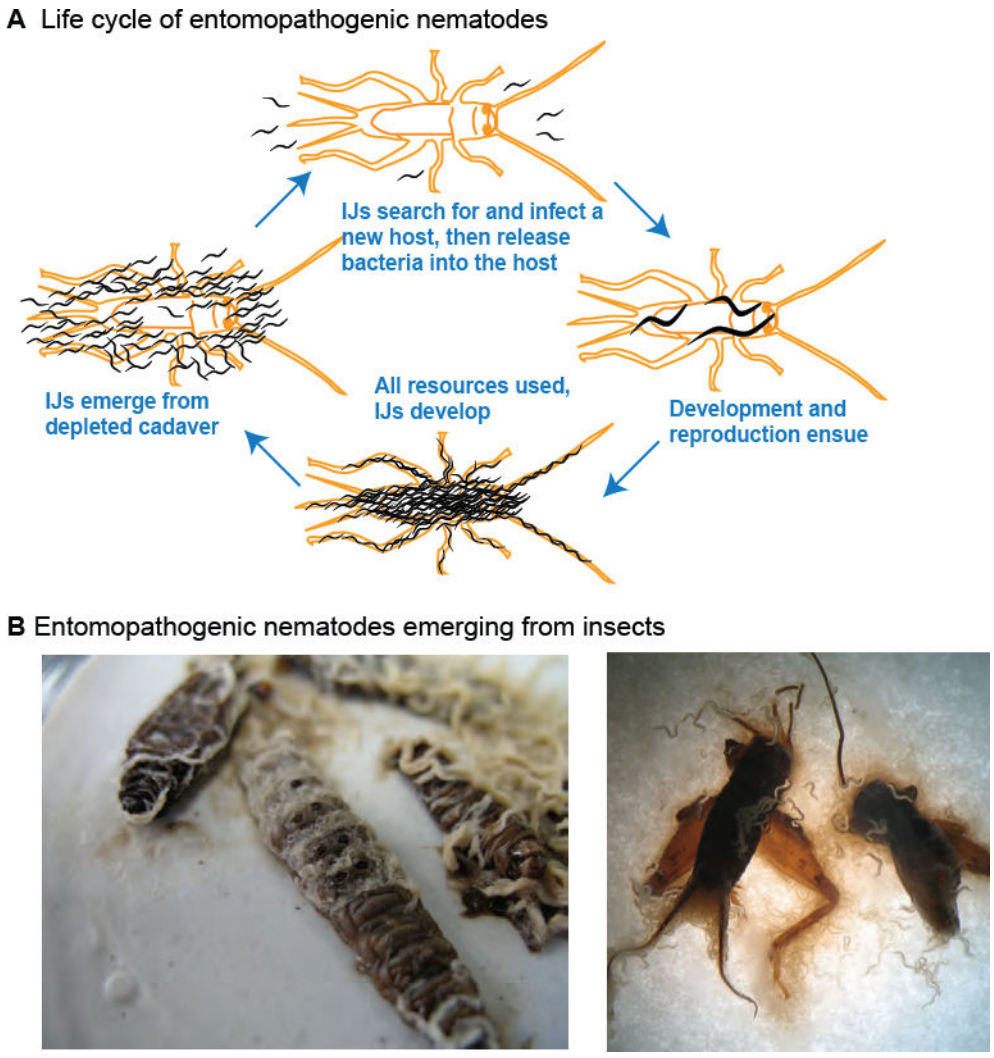

Figure 1.

Life cycle of entomopathogenic nematodes.

(A) The infective juvenile stage seeks out a new host to infect, penetrating into the hemolymph and releasing the pathogenic bacteria it carries. The nematodes develop and reproduce in the nutrient-rich insect, going through several rounds of reproduction, depending on the size of the insect host. As resources deplete, a new generation of infective juveniles form and emerge, seeking new hosts to infect with the pathogenic bacteria they carry.

(B) Pictures showing entomopathogenic infective juveniles emerging from *Galleria mellonella* waxworm larvae on the left and *Acheta domestica* crickets on the right.