INTRODUCTION OF EXOTIC ENOMOPATHOGENIC NEMATODES (Rhabditida: Heterorhabditidae AND Steinernematidae) FOR BIOLOGICAL CONTROL OF INSECTS: POTENTIAL AND PROBLEMS

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ABSTRACT

Interest in the use of entomopathogenic nematodes (Heterorhabditidae and Steinernematidae) as biological control agents of insect pests has grown rapidly in recent years. As a consequence, there has been an increase in the numbers of soil surveys for these nematodes worldwide. These surveys have isolated large numbers of feral nematodes, some of which are new species and strains. It is anticipated that considerable exchange of nematode germplasm will occur between various laboratories. Some of these exchanges may result in the introduction of exotic nematodes into non-native lands. The present paper reviews the potential and concomitant risks of nematode introductions into non-native lands.

RESUMEN

En los últimos años se ha observado gran interés en el uso de los nematodos entomopatógenos de las familias Heterorhabditidae y Steinernematidae para el control de insectos plagas. Como consecuencia, se ha incrementado en todo el mundo el número
Interest in the use of entomopathogenic nematodes for biological control of insect pests is growing rapidly, largely because of the many attributes of these nematodes as biological control agents, including their broad host range, high virulence and reproductive rates, ability to seek out and kill cryptic hosts, quick killing potential within 24-48 h, ease of application, reported safety to nontarget organisms, and improvements in their mass-production, storage, and development of commercial products. This interest led to a sudden wave of soil surveys for these nematodes in England (Hominick & Briscoe 1990), Ireland (Griffin et al. 1991), Germany and Italy (Ehlers et al. 1991), Finland (Vanninen et al. 1989), Hawaii (Hara et al. 1991), New Jersey (Gaugler et al. 1992b), and the Caribbean (K.K.J. et al., unpublished). In addition, earlier surveys were conducted in Australia (Akhurst & Bedding 1986), Czechoslovakia (Mráček 1980), North Carolina (Akhurst & Brooks 1984), Florida (Beavers et al. 1983), Puerto Rico (Roman & Beavers 1982), China, and the Netherlands (cited in Akhurst & Bedding 1986). These surveys have expanded the nematode germplasm available for research and exchange which might increase the likelihood of introducing exotic nematodes into non-native lands. There have been numerous introductions of foreign nematodes into non-native lands. For example, *Steinernema feltiae* (Filipiev) is the most widely used foreign nematode in the United States (R. Georgis, pers. comm.). In addition, *S. carpocapsae* (Weiser) All strain (from the United States) has been introduced into most countries in Europe, except the United Kingdom (R. Georgis, pers. comm.). This paper discusses the potential for introducing exotic nematodes for biological control of insect pests. Specifically, factors that may enhance the likelihood of success of a release are reviewed. Also, the risks of introducing exotic nematodes into non-native lands are defined. It was not the intent of this paper to provide a complete review of factors that limit establishment of nematodes nor those that might pose environmental risks. More complete information on some of these topics is available elsewhere (Poinar 1979, Gaugler & Kaya 1990, Howarth 1991).

**Predictable Biological Control with Nematodes**

Ehler (1990) identified predictability as the most intellectually challenging issue in biological control. Entomopathogenic nematode research is no exception. Gaugler (1988) noted that we need a more complete understanding of nematode interactions with environmental factors that may determine the outcome of nematode releases. Information is lacking on the fate of nematodes introduced into the soil, on factors regulating their population dynamics, on optimal environmental conditions that enhance development of epizootics, on ecological barriers to infection, and on nematode interactions with biotic factors in the soil (Gaugler 1988). Georgis & Gaugler (1991) noted that most failures of entomopathogenic nematodes against Japanese beetle, *Popillia japonica* Newman, grubs were due to the use of an unsuitable nematode strain or environmental conditions. Gaugler (1993) noted that poor field results from releases of genetically improved nematodes were attributable to their poor adaptation to the target host. Goals established for the release of exotic nematodes are similar to those for release
of native nematodes and may vary depending upon the target host and habitat. Generally, however, in agricultural environments, the aim of releases is to reduce and maintain pest populations to noneconomic levels for the duration of the crop. The success of an introduction can be measured in two ways: the effect on the target pest population and crop damage, and persistence in the target habitat. We need to increase our ability to predict the outcome of the release to increase the likelihood of success with exotic nematodes. These goals might be achieved by evaluating the potential effect of a variety of biotic and abiotic factors, and the release strategy on suppression of the target host population and establishment of the nematode.

Factors Limiting Success of Introduced Nematodes

Target Host and Habitat

The success of an introduction will depend upon the biology and behavior of the target host (Kaya 1985). The stage of the target host is of central importance in the nematode-host encounter. It is well known that certain life stages (e.g., larva) are more susceptible to these nematodes than others (e.g., pupa and adult). Success of introductions will also be limited by the availability of the host at the time of the introduction. This is especially true for these nematodes because of their short dispersal capability in soil and their short-lived persistence. Hence, an adequate and constant supply of hosts is needed to enhance recycling at the site of introduction. In addition, the behavioral, physiological, and morphological defensive mechanisms of the target host may affect the potential of these nematodes as biological control agents and the outcome of a release (Gaugler 1988, Kaya 1990).

The habitat of the target host is especially critical in any introduction program. In general, nematode releases have been more successful against below-ground target hosts or hosts in cryptic environments (Begley 1990, Klein 1990) than against above-ground targets on foliage (Kaya 1985, 1986, Begley 1990). This is due primarily to the short persistence of these nematodes on foliage because of the deleterious effects of ultraviolet radiation (Gaugler & Bouah 1978, Gaugler et al. 1992a), and their vulnerability to desiccation and high temperatures (Kaya 1986, Begley 1990 and references therein). However, the limited success of these nematodes against above-ground targets should not dissuade research activity in this area. Innovative approaches and new technologies may help to improve control against above-ground pests (Begley 1990).

Nematode Suitability and Quality

Another important factor that must be considered in any release program with these nematodes is the selection of the candidate nematode for release. Georgis & Gaugler (1991) found that many control failures in the field were due to the use of an unsuitable nematode. It is well known that nematode strains vary in their virulence and infectivity to a target host (Bedding et al. 1983, Malyneaux et al. 1983, Mannion 1992, Mannion & Jansson 1992). For this reason, pre-release studies should be conducted in the laboratory to identify the most virulent nematode(s) for a target host and associated habitat. It should be noted, however, that laboratory results do not always agree with field results. For example, the use of Petri plate assays to screen nematodes and assess virulence is not recommended because it favors nematodes that nictate (Bedding 1990). Mannion & Jansson (1992) found that laboratory results from Petri plate assays concurred with field results (Jansson et al. 1990, 1992, 1993). However, a variety of bioassays, some of which closely resemble the natural environment, should be conducted to select candidate nematodes for field studies (Mannion 1992).
Certain quality control factors need to be addressed to enhance success of the release once a candidate nematode has been selected. Gaugler & Georgis (1992) showed that the method used to mass-produce nematodes had a significant effect on their efficacy in field releases against Japanese beetle. Mass-production methodology was especially important for heterorhabditid nematodes which were shown to be more efficacious when reared *in vivo* or in solid media than when reared in liquid culture. In addition, the length of time that these nematodes have been in storage before release may have a significant effect on the outcome of the introduction (Westerman 1992). Older nematodes with depleted lipid reserves have decreased motility and infectivity which undoubtedly decreases field efficacy.

### Seasonality

Climatic conditions during the experiment will affect the success of any introduction and our ability to predict its outcome. Several studies showed that certain nematodes perform better within a certain temperature regime. Conditions outside the optimum range drastically affect the infectivity and efficacy of these nematodes. For example, Kung et al. (1991) showed that the temperate nematode *S. carpocapsae* survived better at temperatures between 5°C and 25°C than at 35°C, whereas *S. glaseri* (Steiner), a subtropical/tropical nematode (Poinar 1990), survived better at warmer temperatures. Burman & Pye (1980) showed that *S. carpocapsae* displayed a thermal preference for the temperature at which it was reared, infective juveniles actively moved through a temperature gradient towards the temperature that they were acclimated to when cultured. Kung et al. (1991) suggested that persistence of steinernematid nematodes is enhanced in environments similar to the nematode’s climatic origins. Thus, the species and strain of nematode, origin, and its thermal preference will probably affect the predictability of success of a release in a given climatic zone and season of the year. In addition to temperature, precipitation patterns after release, which affect levels of available soil moisture, will have a significant effect on the outcome of a release, especially when precipitation is sporadic and deficient and water holding capacity of soils is poor.

### Application Strategy

Application strategy is a complex factor that can significantly affect the success of nematode releases. In planning a release, researchers need to consider the variety of options: inundative vs. inoculative; periodicity of release; single species or strain release vs. multiple species/strain release; time and placement of application(s); application methodology; and post-application methods to maximize efficacy, motility, and persistence of nematodes. Several of these release strategies were discussed previously (Ehler 1990).

Most field studies have used inundative releases (Georgis 1990), and in most cases, no clear release densities have been recommended. For inundative biological control, the aim is to release a density that will maximize short-term biological control (Ehler 1990). The inconsistency of field trials and poor predictability have hampered our ability to develop release levels. The numbers to release will undoubtedly be affected by several factors, including the numbers of species and/or strains released, the climatic origin of the candidate nematode(s), the quality of the nematode, the biology and behavior of the target host and the nematode, and environmental conditions.

Inoculative releases aim to establish a biological control agent permanently in the target habitat and some studies with nematodes suggested that this strategy has merit (Parkman & Frank 1998, Gaugler et al. 1992b). The success of establishment is depen-
dent upon many of those factors that will limit the success of inundative releases plus the availability of alternate hosts during periods of low host density, a high host-seeking ability of the candidate nematode, and a high level of virulence and recycling.

Another release strategy that might affect the likelihood of success is the periodicity of release. Jansson et al. (1991) showed that a single release of *Heterorhabditis bacteriophora* Poinar was adequate for controlling populations of the sweetpotato weevil, *Cylas formicarius* (Fabricius). Parkman et al. (1993) also showed that a single release was adequate for establishing *S. scapterisci* Nguyen & Smart for control of mole crickets, *Scapteriscus* spp., in northern Florida. Other studies, however, found that multiple releases may be needed (K. Smith, pers. comm.). In general, the periodicity of release needed will vary depending upon the candidate nematode, the target host and habitat, and environmental conditions (Jansson et al. 1991).

The number of species or strains to be released may also affect the likelihood for success. Alatorre-Rosas & Kaya (1990, 1991) showed that steinernematid and hetroorhabditid nematodes compete for hosts. Heterorhabditid nematodes had a competitive advantage when hosts were placed at a greater distance from the inoculation site (Alatorre-Rosas & Kaya 1990). However, when hosts were close to the inoculation site, steinernematids outcompeted hetroorhabditids. Steinernematids also held a competitive advantage over heterorhabditids in Petri plates even when heterorhabditids were introduced 10 hours before steinernematids (Alatorre-Rosas & Kaya 1991). Total mortality was greater when the two nematodes were applied in combination than when the two were applied alone (Alatorre-Rosas & Kaya 1991). To my knowledge, no field studies have been conducted to test their results. Entomopathogenic nematodes have the potential to enable researchers to test this biological control theory in the field (Ehler 1990).

Other factors that will affect the likelihood of success with exotic nematodes include the method of application (manual vs. mechanical applications), time and placement of applications, and post-application methods, such as irrigating, that help to maximize dispersal and persistence of nematodes. Most of these have been discussed previously (Kaya 1985, Gaugler 1988).

**Soil Characteristics**

Soil characteristics have a significant effect on the survivorship, motility, and infectivity of entomopathogenic nematodes (Kaya 1985, 1990 and references therein, Barbercheck 1992). Wallace (1963) stated that the most important factors affecting nematodes are pore size, moisture, oxygen (aeration), temperature, and chemistry of soil solution (pH). Recent studies confirm that persistence and infectivity of these nematodes are limited by soil type (Kung et al. 1990), soil temperature, moisture, ambient relative humidity (Kung et al. 1991). The reader is referred to Kaya (1990) and Barbercheck (1992) for a complete review on the effects of soil ecology on these nematodes. It is important to note, however, that not all entomopathogenic nematodes are affected equally in a given soil environment. Therefore, it is important to know the relationships between survivorship, motility, and infection of the candidate nematode and the target soil environment before release. Matching the appropriate nematode with a compatible soil environment will enhance the likelihood of obtaining a successful introduction.

**Compatibility with Pesticides**

Nematode compatibility with pesticides is a neglected area of research. Because of the diversity of pest complexes that attack most crops, it is likely that an introduced nematode will encounter one or more pesticides. Many biological control programs that
rely on predators and/or parasitoids have been hampered by the lack of compatibility between pesticides and introduced enemies. Compatibility of pesticides with nematodes was studied in turfgrass (Zimmerman & Cranshaw 1990). They found that nematode survivorship in various pesticides differed among nematode species. Surjusin C et al. (1991) also found that tolerance to pesticides differed among nematode species. In general, steinernematids were found to be more tolerant to pesticides than were heterorhabditids. Gaugler & Campbell (1991) found that oxamyl was not compatible with S. carposcapae nor with H. bacteriophora. Kaya (1985) listed several other studies demonstrating compatibility or incompatibility of nematodes and certain pesticides. No generalizations on nematode compatibility with pesticides can be made at this time; thus, the pesticides that a nematode might encounter, and their potential effect on the nematode, should be known before a release to increase the likelihood of success.

Biotic Factors in Soil

Several studies demonstrated that biotic antagonists in the soil can affect the biological control potential of a nematode significantly (Kaya 1990). These nematodes are susceptible to infection by nematophagous fungi (Timpar & Kaya 1992, Timpar et al. 1991) and microsporidians (Kaya 1990); they can be caught by nematode-trapping fungi (Kaya 1990), and preyed upon by mononchid and dorylamoid nematodes (Kaya 1990), various mites (Epsky et al. 1988), and some collemboans (Epsky et al. 1988) and tardigrades (Kaya 1990 and references therein). In addition to antagonists, the outcome of released nematodes might also be influenced by competitors in soil, such as fungi (Barbercheck & Kaya 1990, 1991). They found that total mortality of beet armyworm, Spodoptera exigua Hübner, was greater when entomopathogenic nematodes were combined with a fungus, Beauveria bassiana (Bals.) Vuill., than when each entomopathogen was present alone; however, due to interspecific competition for hosts, the fungus reduced the level of mortality achieved by the nematode more than the nematode reduced the mortality due to the fungus (Barbercheck & Kaya 1991).

Risks of Introducing Exotic Nematodes

As mentioned earlier, factors limiting the success of exotic nematodes are no different from those that limit releases of native nematodes. However, because of the increased nematode germplasm currently available from several surveys and the potential for exchange and release of these nematodes, the potential environmental effect of release of exotic nematodes must be weighed carefully before release.

Howarth (1991) discussed environmental effects of classical biological control programs and indicated that certain biological parameters that might help or hinder an exotic organism's risk potential need to be defined in order to weigh the risk of an introduction. There are several risks associated with introducing exotic nematodes into non-native lands. Some of these risks are similar to those described by Howarth (1991). The most important factors that affect the level of risk for introducing these nematodes include: the potential for range expansion; the host range of the candidate nematode and the effect of its encounters with non-target organisms (including their threat to human and animal health); the permanence of the introduction and the vulnerability of the target habitat; the nematode's relationship with associated bacteria; and their effect on community and ecosystem dynamics. It should be noted that any introduction that results in establishment of nematodes will likely affect the environment (Ehler 1990). Although Ehler (1990) restricted his criterion to only those introductions that result in permanent establishment, in certain cases, especially when inundative releases might be conducted in vulnerable habitats, a significant effect could occur even without a
permanent establishment of the nematode. Although it is generally accepted that these nematodes pose little environmental risk, considerably more data are needed before any generalizations can be made (Ehler 1990).

Range Expansion

The potential risk of an introduction might be affected by the nematode's ability to expand its range and disperse beyond the site of introduction. This risk is difficult to weigh because few studies have been conducted.

Active dispersal of this nematode in soil is well documented (Moyle & Kaya 1981, George & Poinar 1983a,b,c, Poinar & Horn 1986, Mannion & Jansson 1993). It is unlikely that this mode of dispersal is a significant threat for range expansion because of the limited distances that these nematodes can move. Mannion & Jansson (1993) showed that a small percentage of G. mellonella larvae placed 60 cm from inoculation points became infected up to 4 months after application suggesting that few nematodes dispersed 60 cm laterally from the inoculation site.

Passive movement of these nematodes poses a more serious threat for range expansion. Movement of plant-parasitic nematodes on farm equipment, etc., is well known; thus, similar modes of dispersal that move soil by humans might also help facilitate movement of these nematodes. Several researchers speculated that entomopathogenic nematodes could disperse beyond the infection site on mobile adult insects before adults become infected (Glaser & Farrell 1986, Finney & Walker 1977). Timper et al. (1988) showed that S. carpocapsae dispersed up to 11 m from the site of infection on infected S. exigua adults. They suggested that this type of dispersal could help account for the widespread dispersal of these nematodes locally and perhaps worldwide. Parkman & Frank (1992) showed that newly-infected mole crickets dispersed the nematode S. scapterisci. Mobile larvae might also aid in dispersal before infection (Molyneux et al. 1983). Epsky et al. (1988) showed that megastigmatid and oribatid mites could serve as phoretic hosts and help to disperse S. carpocapsae.

Host Range and Impact on Nontarget Organisms

Entomopathogenic nematodes are considered to have a broad insect host range (Laumon et al. 1979, Poinar 1979, 1990, Gaugler 1981). However, in nature the host range of these nematodes may be restricted to some extent by behavioral and ecological barriers. For example, not all entomopathogenic nematodes have a broad host range. Steinernema scapterisci is highly specific for mole cricket hosts, Scapteriscus spp. (Nguyen & Smart 1991). Also, as mentioned earlier, virulence differs among nematodes in a variety of insect hosts. Host range may also be restricted by susceptibility of the life stage encountered by these nematodes after release. In addition, although many insects are susceptible to these nematodes in the laboratory, not all are likely to be infected in nature (Smart 1992). Also, although nematode-nontarget organisms encounterers are inevitable, the result of these encounters will not be the same for all nematodes.

Several studies showed that these nematodes do not infect birds or mammals (Poinar 1990 and references therein). However, Kermarrec & Mauléon (1985) showed that these nematodes have the potential to infect young toad tadpoles of Bufo marinus (L.). More recently, Kermarrec et al. (1991) also showed that a lizard, Anolis marmoratus Duméril & Bibron, was affected adversely by some of these nematodes. Poinar and Thomas (1988) showed that S. carpocapsae and Heterorhabditis bacteriophora Poinar could kill young tadpoles of Hyla regilla Baird & Girard and Xenopus laevis (Daudin).

Ishibaishi & Kondo (1986) found that applications of steinernematid nematodes increased native populations of Rhabditida and decreased populations of plant-parasitic
nematodes. Other research has shown that introduction of exotic nematodes may affect populations of nontarget beneficial insects (Kaya 1984, 1986, Kaya et al. 1982, Laumond et al. 1979).

Others found that these nematodes have little effect on nontarget invertebrates (Poinar 1979 and references therein). Ishibashi et al. (1987) found that repeated inoculation of soil with S. carpocapsae did not affect populations of collemboles and mites adversely. Similar results were found by Klein & Georgis (1992). Georgis et al. (1991) showed that applications of entomopathogenic nematodes did not affect the numbers of nontarget invertebrates (Carabidae, Staphylinidae, Gryllidae, Histeridae, Collembola, Gamasida, Actinedida, and Oribatida) adversely in the soil compared with applications of chemical insecticides. However, in their study, all invertebrates were pooled by their respective family and the effect of nematode releases on individual species of nontarget invertebrates was not determined. Others showed that these nematodes did not adversely affect populations of an earthworm (Capinera et al. 1982) and honey bees (Kaya et al. 1982). Nickle et al. (1988) suggested that research on the effect of these nematodes on nontarget invertebrates should be considered if an introduction of an exotic nematode is planned in the United States. Despite the evidence, it is premature to conclude that these nematodes are safe for nontarget invertebrates in all environments (Akhurst 1990). Too few long-term studies on the effects of these nematodes on the invertebrate fauna in an environment have been conducted to draw any conclusions.

Effect on Community Dynamics and Displacement of Native Nematodes

Hominick & Reid (1990) raised the question: Do entomopathogenic nematodes influence the plant communities that exist in a given area through their effect on the soil herbivores? A recent study showed that these nematodes were most common in the U.K. in roadside verges, where there were mixed and diverse plant communities (Hominick & Bristow 1990). Insect herbivores affect early-stage succession (Brown & Gange 1989). Thus, it is conceivable that these nematodes might exert an impact on succession of communities by affecting soil herbivores (Hominick & Reid 1990). If these nematodes play a significant role in successional changes in plant communities, then the effect of an introduction would extend beyond nontarget organisms in soil communities to entire ecosystems.

As mentioned earlier, nematode releases may affect populations of native plant-parasitic and rhabditid nematodes (Ishibashi & Kondo 1986). A logical question one might ask is: Can releases of exotic nematodes displace or replace populations of native entomopathogenic nematodes? Displacement of native nematodes is an unknown risk, but one that should be contemplated before releasing a newly discovered nematode species into a non-native area. Pre-release studies on competition between native and exotic nematodes for hosts would help to evaluate this potential risk.

Permanence of Introduction and Vulnerability of Target Habitat

Howarth (1991) noted that introduced enemies that persist for long periods of time have a greater chance of affecting the environment adversely. Most field studies on entomopathogenic nematodes have shown that these nematodes persist poorly. Nematode persistence in soil is a function of host availability, host-seeking ability, survivorship, reproduction, availability of alternate hosts, time and method of application, quality of nematodes, and soil biotic and climatic factors (Kaya 1990 and references therein). Recent studies, however, demonstrated that these nematodes have the ability to persist in field soil well beyond the time of application and in some cases beyond the duration of a suitable habitat. Jansson et al. (1991, 1993) showed that heterorhabditid
nematodes, *H. bacteriophora* and *Heterorhabditis* sp., persisted for over 230 days after application in sweet potato fields in southern Florida. Klein & Georgis (1992) found that *H. bacteriophora* persisted through the winter in turfgrass plots for up to 290 days after application. Parkman et al. (1993) showed that *S. scapterisci* persisted for over 5 years after application in northern Florida.

Vulnerability of the target habitat was also listed as a factor that might affect the level of risk in classical biological control programs (Howarth 1991). This is probably also true for entomopathogenic nematodes. Island habitats have been reported to be very vulnerable (Howarth 1991). Hominick (1991) suggested that the high incidence of heterorhabditid nematodes near the coasts of many Caribbean and Pacific islands, as well as in the U.K., might be due to their inadvertent movement by man in ship ballast. The effect of these inadvertent introductions is not known, but is assumed to be minimal because of the low incidence of these nematodes in other habitats on these islands (Hara et al. 1990, Hominick & Briscoe 1991, Griffin et al. 1991, R.K.J. et al., unpublished). The potential for these nematodes affecting the environment probably increases with a decrease in latitude. Environmental conditions in tropical climates are more conducive for nematode establishment due to more favorable soil, temperature, and precipitation patterns, an abundance of hosts throughout the year, especially coleopterans and lepidopterans which are very susceptible to these nematodes (Capinera & Epsky 1992).

**Relationship with Bacteria**

Another risk of introducing exotic nematodes might be their relationship with bacteria. This is especially true for previously unrecorded nematodes that were recently isolated and for which there is no information on their symbiotic bacteria. Currently, the taxonomy of *Xenorhabdus*, especially *X. luminescens*, is incomplete. Akhurst & Boemare (1990) noted that *X. luminescens*, the bacterium associated with *Heterorhabditis*, should probably be divided into several taxonomic groups. Similarly, the taxonomic relationships between the bacteria and the Steinernematidae are not completely clear (Akhurst & Boemare 1990). Because at least one species of *Xenorhabdus* (reported as *X. luminescens* [DNA hybridization group 5] but known to be a new species [Akhurst & Boemare 1990]) was isolated from human wounds (Farmer et al. 1989), the symbionts of newly discovered nematodes may complicate government insecticide registration in some countries. However, in reality, the symbiotic bacterium probably poses little danger to the environment because it is not found normally outside the host or the nematode. It was suggested that release of foreign nematodes into the United States should not be considered until the nematode and its bacterial association are known (Coulson et al. 1991).

**Summary and Future Outlook**

Introductions of exotic entomopathogenic nematodes may have potential for biological control of insects in non-native lands. As shown by Bedding & Akhurst (1974), classical biological control can be successful with nematodes. They showed that a siricorn wood wasp could be controlled with releases of the exotic nematode *Bodingia* (= *Deladenus*) *siricidicola* Blinova & Korenchenko with little effect on nontarget organisms. A more recent study also indicated that release of an exotic nematode, *S. scapterisci*, from South America against mole crickets, *Scapteriscus* spp., in Florida has potential for controlling these insects (Parkman et al. 1993).

Because entomopathogenic nematodes have a limited ability to expand their habitat range once introduced, usually persist for short periods of time in most habitats, reportedly have little effect on nontarget organisms, and pose a low risk to man and animals,
introductions of exotic nematodes should be encouraged. However, because we know virtually nothing about recently isolated new species of *Heterorhabditis* and *Steinernema* and their associated bacteria, release of these nematodes should await the results of more rigorous pre-release studies on identification, host range, affect on nontarget organisms, etc. Guidelines for importation, movement, and release of exotic entomopathogenic nematodes in the United States are available (Nickle et al. 1988, Coulson et al. 1991). It should be noted, however, that many researchers studying these nematodes advocate less restrictive guidelines (Parkman et al. 1992, Smart 1992) than those proposed by Nickle et al. (1988) and Coulson et al. (1991). It is important to emphasize with regard to all introductions of exotic nematodes that the success of an introduction will depend upon all of the biotic and abiotic factors described above. Thus, researchers should consider these factors very carefully when planning releases of exotic nematodes so that we can better predict the outcome.

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WHEN DOES INVESTING IN CLASSICAL BIOLOGICAL CONTROL RESEARCH MAKE ECONOMIC SENSE?

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ABSTRACT

A simple model is presented which calculates the expected net benefits of classical biological control projects. Estimates of project cost, length, chance of success, and the time value of money are used to calculate the potential benefit necessary to economically justify investment in a typical project. The potential benefit is about $62 thousand per year. The effects of changing key model parameters on the level of the required benefit are explored.