

ANWAR L. BILGRAMI

BIOLOGICAL CONTROL POTENTIALS OF PREDATORY NEMATODES

*Department of Entomology, Rutgers University,
New Brunswick, NJ 08901, USA*

Abstract. Biological control potential of predatory nematodes is evaluated and discussed in the following chapter. Attributes of a successful biological control agent such as mass production, reproductive potential, longevity, compatibility with agrochemicals, safety to non-target organisms, prey search ability, environmental adaptability, dispersal and persistence capabilities etc., are enumerated. Prey searching and feeding mechanisms, prey preferences, ecology, biology and conservation of predatory nematodes and prey resistance and susceptibility to predation are elaborated and supplemented with the list of plant-parasitic nematodes recorded as prey to various species of predatory nematodes.

1. INTRODUCTION

Air, land and water are alarmingly polluted to the extent that several sensitive species are becoming extinct at the rate never experienced before on earth. Pesticides and chemicals, inextricably associated with us from fabric to food, pose a major threat to our lives. Their adverse effects on human and animal populations, pest resistance and continued ravage on one third of food produced worldwide, call for including nature's own enemies to manage plant pests, including phytoparasitic nematode populations.

Biological control of pests is as old as agriculture. Centuries ago, ducks were used to consume pests, a technique still adopted in China. The first known biological control strategy was implemented in 1762, when a Mynah bird was taken from India to Mauritius to control locusts. However, the landmark in biological control was achieved in 1880 when ladybird beetles were used to control scale insects in citrus plantations. Biological control may be defined as the "*action of parasites, predators and pathogens in maintaining other organism's population density at a lower average than would occur in their absence*". It may be elaborated further as "*any condition under which or practice whereby, survival or activity of a pathogen or pests is reduced through the agency of other living organism*". This is referred to as "*Natural biological control*" since it involves predators and pests without human intervention. However, if "*the use of predators and parasites are induced to multiply and disseminated by human efforts*" it would be referred to as "*induced inundated biological control*". With the advent of biotechnology, the concept of biological

control needs to be redefined as “*the use of nature and/or modified organisms, genes or gene products to regulate or reduce pests in favour of human and animal populations, and agricultural crops besides protecting other beneficial organisms*”. Biological control measures are, therefore, both corrective (e.g., chemical) and preventive (e.g., cultural) in nature. Preventive, as they help evading the disease and corrective because if the disease is already set in, it corrects the malady by reducing pest populations.

The advocacy of nematode biocontrol dates back to several decades, but its usefulness was brought to sharp focus only recently. Initial research by Linford and Oliviera (1937, 1938), though empirical, generated interest in using amendments to control plant-parasitic nematodes. How soil microorganisms/organic amendments reduce plant-parasitic nematodes may provide basic informations to understand nematode biological control. Two hypothesis were proposed to explain why organic amendments mostly help in reducing plant-parasitic nematodes: (1) the products released by amendments are directly toxic to plant-parasitic nematodes and (2) the organic compounds initiate a succession of events which favour the populations of indigenous biological control agents.

Biological control achieved success in Entomology, Plant Pathology and Insect Nematology. Little is achieved with phytoparasitic nematodes except predaceous and parasitic fungi, which contributed 73% of the total research efforts (Table 1). Predatory nematodes attracted 13% research effort whereas the other organisms ranged between 1–6%.

Table 1. Research on different biological control agents with reference to predatory nematodes.

<i>Biocontrol organism</i>	<i>Research efforts (%)¹</i>
Predaceous Fungi	56
Parasitic Fungi	17
Predaceous Nematodes	13
Bacteria	6
Tardigrades	1
Protozoa	<1
Rickettsiae	<1
Collembola	<1
Viruses	<1
Turbellarians	<1
Mites	<1
Enchytraeids	<1

¹Assessed from examination of 1000 papers in the year 2002.

Research carried out during the last 10–15 years generated interest in evaluating the role of predatory nematodes as nematode biocontrol agents. The use of predatory nematodes is challenging because both predatory and parasitic nematodes are small in size and inhabit soil. Biology, behaviour, food and feeding preferences, prey relationships, together with other ecological parameters are important to fully evaluate their biological control potentials.

2. BIOLOGICAL CONTROL ATTRIBUTES

Effectiveness of predatory nematodes as biocontrol agents depends upon the following characteristics.

Culture: predatory nematodes to be used as biocontrol agent should be easily and cheaply culturable on commercial scale (e.g., diplogasterid predators).

Reproductive potential: predatory species must have a high reproductive rate in order to maintain population at higher densities (i.e., diplogasterid predators). Occasionally, high reproduction adversely affects efficiency, due to high energy requirement. Thus, a judicious balance between reproductive and infective potentials of predatory nematodes needs to be achieved.

Longevity: as a successful biocontrol agent, a predatory nematode should be characterized by significant longevity and stability, so that it can be stored without appreciable loss of its predation capacity.

Application: compatibility of predatory nematodes with agrochemicals and standard farm practices is extremely important in order to achieve successful application and significant control.

Safety to non-target organisms: Although most biocontrol agents are non-pathogenic, the safety of non-target organisms e.g., plants, humans and other beneficial organisms must be kept in mind. The ability of nematodes to avoid predation on organisms other than the target would contribute to its success as an efficient biocontrol agent.

Searching capability: prey searching ability is an important attribute that affects predator's mobility, predation and biocontrol potential. Predatory nematodes possessing efficient searching ability (e.g., diplogasterids) would be more effective as biocontrol agents than those lacking prey search ability (e.g., mononchs).

Environmental adaptability: Any predator that adapts and tolerates existing and changing environmental conditions as well as any species capable of ecological and temporal compatibility would result best fit to act as an efficient biocontrol agent.

Temporal compatibility: perfect temporal compatibility between predatory and pest nematodes is another important attribute that contributes towards the success of biological control. Temporal compatibility synchronizes predator-prey life cycles and eliminates time gaps that allow pests to escape predation.

Dispersal and persistence capability: ability to disperse, persist, survive and reproduce under adverse conditions including absence of prey are ideal candidates for nematode management. Dual feeding habits (e.g., diplogasterid feeding on prey and bacteria) help predators to thrive equally well on alternate food (e.g., diplogasterid predators feed on bacteria in prey absence). Ability of predatory

nematodes to reduce parasitic-nematode population within a short time span is also important for biocontrol (e.g., diplogasterid predators). To reduce pest populations below noxious levels, high predation ability and long predators persistence enhance biocontrol efficiency.

Broad spectrum efficiency: monophagous (an undesirable biological control trait) predators may be efficient regulators, but they may allow development and establishment of other noxious nematode species. It is desirable that predatory nematodes should possess a broad host range, in order to harm a diverse spectrum of noxious nematodes.

Capacity to produce toxic metabolites: Predatory nematodes that produce toxic secretions to kill or inactivate pest organisms (e.g., *Seinura* injects toxic substances to inactivate its prey) possess yet another attribute of a successful biocontrol agent.

Hyperparasitism: this trait significantly affects biological control potential. Predatory nematodes (e.g., mononchs) resorting to cannibalism in absence of preys (an example of hyperparasitism) can never represent an optimal good choice as other nematodes biocontrol agent. Cannibalism is a condition in which predators feed on conspecific individuals, thus reducing biological control potential.

2.1. Prey Capturing and Feeding Abilities

Predatory feeding is divided into different phases (Fig. 1), namely encounter with prey, attack response, attack, extra corporeal digestion and ingestion (Bilgrami & Jairajpuri, 1989b).

Encounter with prey: this phase is established either by willful movements of predators in response to kairomones emitted by the prey (diplogasterid, dorylaim or nygolaim predators) (Bilgrami & Jairajpuri, 1988a; Bilgrami, & Pervez, 2000; Bilgrami, Pervez, Yoshiga, & Kondo, 2000; Bilgrami, Pervez, Kondo, & Yoshiga, 2001) or by a chance contact (e.g., mononchs) (Grootaert & Maertens, 1976) (Fig. 1). Cutting and sucking type (e.g., *Mononchoides*, *Butlerius*) or stylet-bearing predators (e.g., *Mesodorylaimus*, *Aquatides*) establish contacts with the prey in response to attractants (Bilgrami, 1997). Predator attraction towards prey and aggregation around the feeding sites suggest an important role of prey secretions in establishing predator-prey contacts. Unlike other predatory groups, diplogasterids are attracted towards bacteria (Bilgrami & Jairajpuri, 1988a).

Attack response: Attack response is generated as a result of head probing, feeding apparatus movements and oesophageal pulsations. Prey contacts at right angles are necessary to initiate an attack (Fig. 1) as glancing contacts or contact other than right angles do not result in successful attacks. Attack response varies from predator to predator, it may be aggressive as in *Prionchulus* or *Mylonchulus*, vigorous but confined in *Labronema*, gradual and restricted in *Aquatides* or *Dorylaimus*. Attacks always followed probing of prey, which may be limited to a rapid side-to-side lip rubbing (*Mononchus*), vigorous (*Mononchoides*) or just an head shaking and lip rubbing against prey's body (*Butlerius*).

Attack: predators cut or penetrate the prey cuticle by side-to-side lip rubbing with simultaneous movements of the feeding apparatus (Bilgrami & Jairajpuri, 1989b). If a predator fails to puncture the cuticle it searches another spot on the prey

body or reverts back to search for another prey. The prey is attacked by the stylet (e.g., *Mesodorylaimus*, *Discolaimus*, *Seinura*), mural tooth (e.g., *Aquatides*), dorsal tooth (e.g., *Mylonchulus*), onchia (*Actinolaimus*), teeth (e.g., *Ironus*) or by the combined actions of a movable dorsal tooth and high esophageal suction (e.g., *Mononchoides*, *Butlerius*). *Aquatides* and *Dorylaimus* puncture prey cuticle by gradual and intermittent thrusting of the stylet (Shafqat, Bilgrami, & Jairajpuri, 1987) whereas *Labronema* achieves puncturing through quick stylet movements (Wyss & Grootaert, 1977) (Fig. 2). *Diplenteron* (Yeates, 1969), *Butlerius* (Grootaert, Jaques, & Small, 1977) or *Mononchoides* (Bilgrami & Jairajpuri, 1989b) use their movable dorsal tooth and esophageal suction to slit open the prey cuticle (Fig. 2). *Mononchus*, *Iotonchus* and other mononchs engulf and swallow their prey whole or shred their body prior to feeding (Fig. 2) (Bilgrami, Ahmad, & Jairajpuri, 1986). *Dorylaimus* needs 6-8 thrusts to penetrate the prey cuticle (Shafqat et al., 1987) whereas *Labronema* and *Aquatides* requires 5-6 stylet thrusts (Wyss & Grootaert, 1977). *Mesodorylaimus* needs fewer stylet thrusts (6-9) than *Aporcelaimellus* (7-12) (Khan, Bilgrami, & Jairajpuri, 1991) to perforate the prey cuticle. *Seinura* injects toxic esophageal secretions to paralyze its prey (Hechler, 1963). Other stylet bearing predators disorganize internal body organs of prey to make them immobile before initiating feeding. *Mononchs* inactivate their prey by holding them firmly with the buccal armature and high esophageal suction.

Extracorporeal digestion: stylet bearing predators partially digested their food outside the oesophagus prior to ingestion since their lumen is too narrow to ingest large food particles, a phenomenon known as extracorporeal digestion in plant parasitic (Wyss, 1971) and predatory nematodes (Bilgrami & Jairajpuri, 1989b). Mononchs do not pre-digest food since they can swallow a prey whole or ingest its pieces through the wide oral aperture. In contrast, diplogasterid predators partially digest food molecules prior to ingestion, by releasing esophageal gland secretions (Bilgrami & Jairajpuri, 1989b). Complex food globules are broken down into small particles before they are ingested through stylet lumen en route to the intestine. *Diplenteron*, *Dorylaimus*, *Aquatides*, *Seinura*, *Mononchoides* and other predators show extra corporeal digestion of food molecules.

Ingestion: most species of mononchs engulf prey or ingest it after shredding into pieces (e.g., *Iotonchus*) (Fig. 2) but few (e.g., *Mylonchulus*) feeds by cutting and sucking their prey (Bilgrami et al., 1986). Swallowing of prey is supported by the esophageal muscle contractions that pull prey into the buccal cavity through vertically positioned plates. Some individuals show periods of inactivity after devouring an entire prey, while others initiate further attacks. Stylet bearing predators cannot engulf their prey or shred it into pieces, but penetrate and rupture the internal body structures by making sideways movements of the feeding apparatus. Prey contents are ingested through the esophago-intestinal junction by simultaneous relaxation and contraction of the esophageal bulb. Once the contents are ingested, predators detach their lips from the prey, retract feeding apparatus and move in search of another prey. Stylet bearing predators also feed upon the eggs of other nematode species but not conspecific eggs. When in contact with conspecific eggs, these predators probe in an exploratory fashion by making side-to-side lip rubbing but cause no harm to the eggs (Esser, 1987). Diplogasterids could devour

intact first stage juveniles of small prey nematodes (e.g., *Acrobeloides* or *Cephalobus*) but must cut larger preys into pieces to feed. The process of food ingestion in *Neoactinolaimus*, *Ironus* or *Thalassogenus* is identical.

Predators struggle among themselves to feed if their number exceeds 3 at a feeding site. Aggregation at feeding sites is common in dorylaim (Bilgrami et al., 2000), nygolaim (Bilgrami et al., 2001) and diplogasterid predators (Bilgrami & Jairajpuri, 1988a) (Fig. 2). Up to eight diplogasterid predators were found aggregated at the feeding site. Aggregation is most pronounced at low prey densities, allowing predators to quickly finish feeding before hunting other preys.

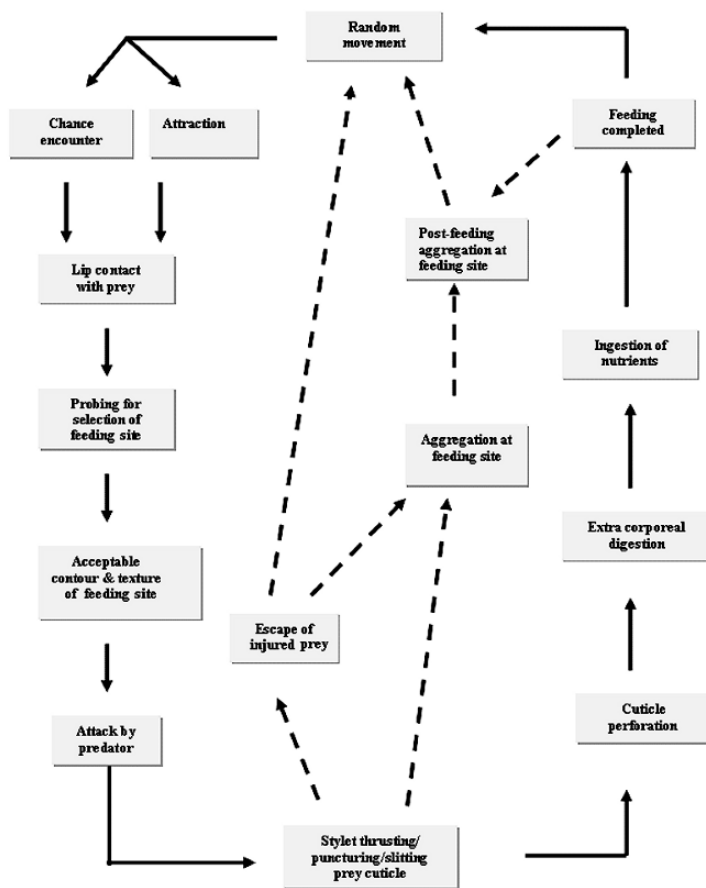


Figure 1. Capturing and feeding mechanisms in predatory nematodes.

2.2. Prey Resistance and Susceptibility to Predation

Successful biological control could be achieved if predators possess high strike rate and prey nematodes are highly susceptible. Cohn and Mordechai (1974), Grootaert et al. (1977), Small and Grootaert (1983) and Bilgrami and Jairajpuri (1989a) differentiated prey nematodes depending upon their abilities to resist predation. The ability of prey nematodes to defend themselves against predator's onslaught varies from species to species.

Resistance to predation is due to the coarse body annulations (e.g., *Hemicriconemoides*), thick or double body cuticles (e.g., *Hoplolaimus*), gelatinous matrix, toxic body repellents (e.g., *Helicotylenchus*) or rapid undulatory body movements (e.g., *Rhabditis*). Bilgrami and Jairajpuri (1989a) proposed the following equations to determine predator strike rate and prey resistance and susceptibility to predation.

$$\text{Strike rate of predators (\%)} \quad \text{SR} = (\text{EA}/\text{A}) \cdot 100$$

$$\text{Prey resistance (\%)} \quad \text{PR} = (\text{EA}-\text{AW})/\text{EA} \cdot 100$$

$$\text{Prey susceptibility (\%)} \quad \text{PS} = 100 - \text{PR}$$

Where: SR = strike rate of predators; PR = prey resistance; PS = prey susceptibility; EA = number of encounters of predators with prey resulting into attack; AW = number of attacks by predators resulting into prey wounding; A = total number of encounters with the prey.

2.3. Prey Preference

Prey preference is a key feature for the selection of a biological control agent. A broad or indiscriminate host/prey range, as is the case for many predators, can be an undesirable feature in a predator intended for field release. A highly specific predator, on the other hand, limits its effectiveness against target species and mass culturing. Prey preference is determined either from the chance observations in petri dishes or from the analysis of preserved materials. Mononchs are broad in prey specificity as they engulf all types of organisms including nematodes, rotifers, protozoa, oligochetes and other invertebrates (Table 2) (Bilgrami et al., 1986). They are rapacious, with reports of a single individual mononch killing up to 83 cyst nematode (*Heterodera*) per day; another individual ingested 1332 preys over its life span (Steiner & Heinly, 1922).

In a recent study Bilgrami, Gaugler, and Brey (2005) showed prey preference of a predatory nematode in choice and no choice experiments (Fig. 3). They proposed method to determine coefficient of preference based on predators rejection or acceptance of a prey and prey choices they were given. Coefficient of preference is based on the probabilities of success (prey accepted = proportion of one prey killed higher than the other in a prey combination) and failures after prey rejected (proportion of one prey killed less than the other in a prey combination in relation to the number of events, number of combinations for one species i.e., ten) (Table 3) (Bilgrami et al., 2005). Prey preferences were designated as positive (more prey killed) or negative

(fewer prey killed) for the sake of convenience and comparison. Prey rejected does not mean that no prey was killed or eaten. Coefficient of preference, referred to as positive (prey accepted) and negative (prey rejected) ranged between 0 to + 1 and -1 to 0 respectively. Prey species having coefficient of preference approaching + 1 were highly accepted and those approaching - 1 as rejected. Based on Table 3, the coefficient of preference (Table 4) for each species was calculated as follows:

$$\frac{\text{Mean prey accepted (\%)} - \text{Mean prey rejected (\%)}}{\text{Mean prey accepted (\%)} + \text{Mean prey rejected (\%)}}$$

Table 2. Analysis of intestinal contents of mononchs (from Bilgrami et al., 1986).

Predators	Observed	Total	Specimens containing prey*						
			D	T	F**	NI	C	MO	MG
<i>Parahadronchus</i>	164	112 (68%)	42	48	68	48	21	38	14
<i>Mononchus</i>	198	87 (44%)	22	24	55	33	19	10	23
<i>Miconchus</i>	34	15 (44%)	10	8	15	6	3	4	3
<i>Clarkus</i>	62	26 (42%)	4	6	17	8	4	8	8
<i>Prionchulus</i>	105	32 (30%)	18	20	22	24	16	12	0
<i>Sporonchulus</i>	59	16 (27%)	4	6	16	8	7	3	6
<i>Coomansus</i>	24	5 (21%)	4	5	4	4	2	1	0
<i>Iotonchus</i>	173	75 (43%)	50	49	70	52	24	24	20
<i>Mylonchulus</i>	190***	0	0	0	0	0	0	0	0
Total	816	368 (43%)	154	166	277	184	96	100	74

* D = Dorylaims; T = Tylenchs; F = free living; NI = not identified; C = cuticular parts; MO = mononchs of other genera; MG = mononchs of same genera.

** Includes monohysterid, diplogasterid and rhabditid nematodes.

*** Not included in the total as no specimen of this genus had prey in the intestine.

2.4. Ecology

Ecological studies revealed significant generic diversity in predatory nematodes (Bilgrami et al., 2000; Bilgrami, Khan, Kondo & Yoshiga, 2002; Bilgrami, Wenju, Wang, & Qi, 2003). Diversity up to 32% was recorded in the presence of other nematode species (Bilgrami et al., 2003). At the nematode community level, plant-parasitic nematodes dominated but predatory species constituted maximum biomass (Bilgrami et al., 2000, 2003). The positive correlation of predators with plant-parasitic species suggested that the latter represent a suitable food source for predatory nematodes. Such a correlation also indicates a role of predatory nematodes as effective biocontrol agents. In another study Bilgrami et al. (2000) showed predominance of predatory over plant-parasitic and bacteriophagous nematodes in a

deciduous forest. Predatory nematodes constituted a major component of the nematode community due to their abundance, moderate to high density and maximum biomass. Positive correlation between predatory and other nematode species suggested density dependent regulation.

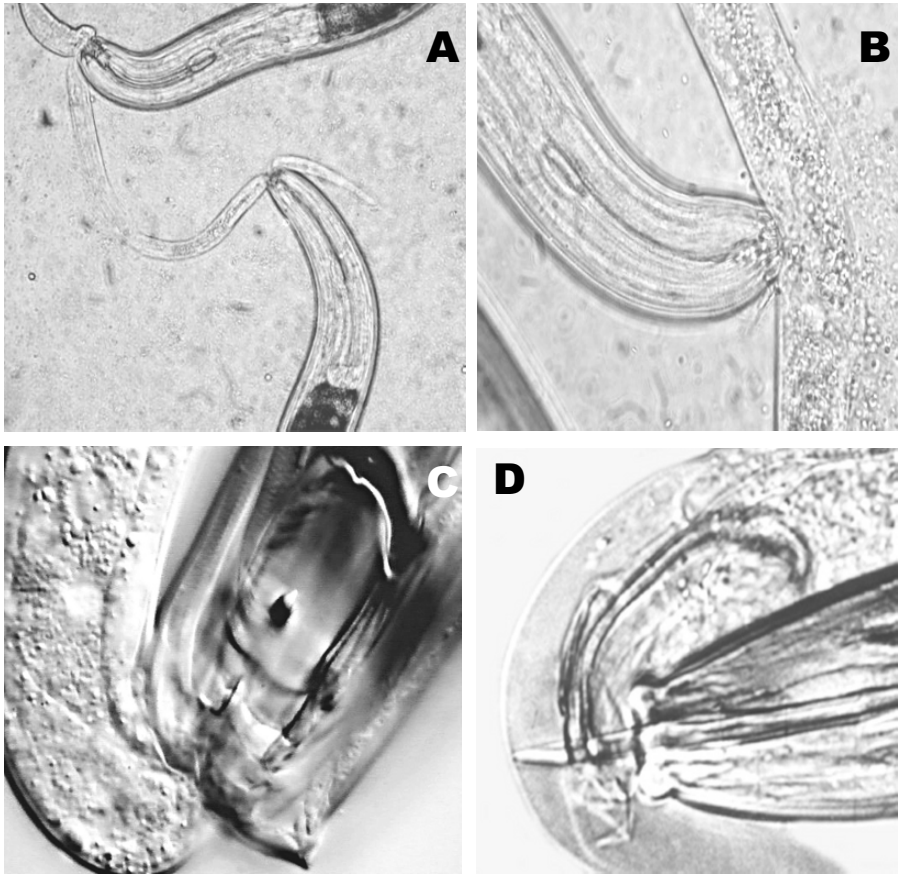


Figure 2. Predatory nematodes feeding activities. (A) two individuals of *Mononchoides gaugleri* (diplogasterid) feeding on the same prey. (B) *M. gaugleri* feeding on a prey. (C) *Anatonchus tridentatus* (mononch) ingesting *Panagrellus redivivus*. (D) *Labronema vulvapapillatum* (stylet bearing predator) sucking prey contents.

Entomopathogenic nematodes feed on specific symbiotic bacteria within the host cadaver. Diplogasterid predators differ from entomopathogenic species in one fundamental way: under natural conditions, they feed on bacteria besides preying nematodes (Pillai & Taylor, 1968; Yeates, 1969; Jairajpuri & Bilgrami, 1990; Yeates, Bongers, De Goede, Freckman, & Georgieva, 1993). The ability of diplogasterids to “switch” between predator and microbivore feeding modes rests in the anticipated

ability to survive periods of low prey densities. Switching behaviour buffers predator populations, and thereby serves as a “powerful stabilizing mechanism” (Hassell, 1978).

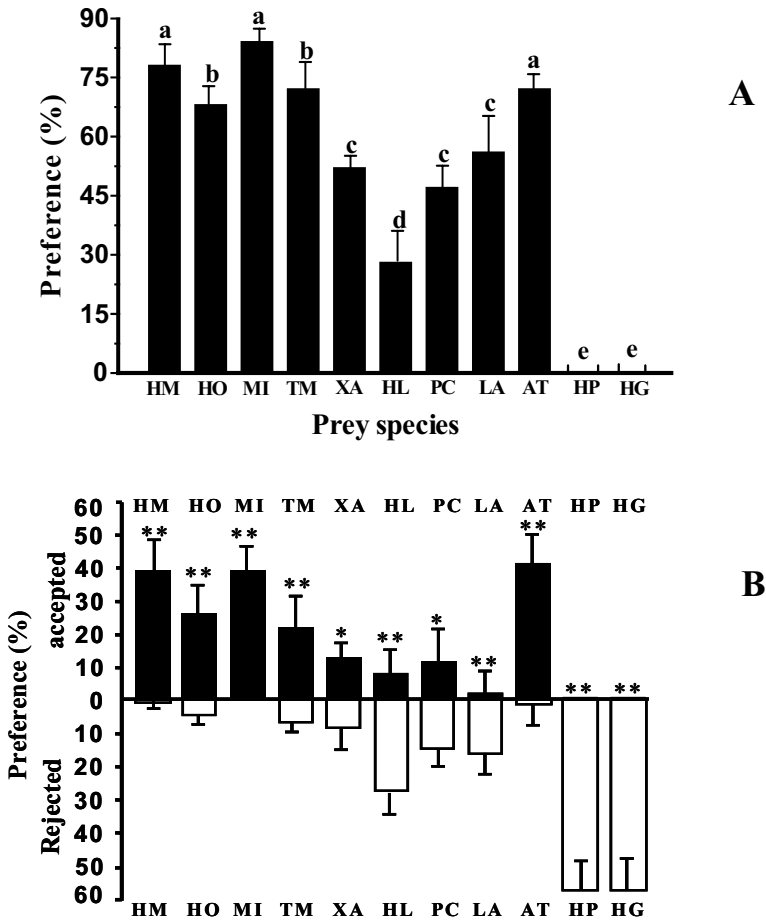


Figure 3. Prey preference by *Mononchoides gaugleri* in no-choice (A) and choice experiments (B). HM = *Heterodera moths* J_2 ; HO = *Hirschmanniella oryzae*; MI = *Meloidogyne incognita* J_2 ; TM = *Tylenchorhynchus mashhoodi*; XA = *Xiphinema americanum*; HL = *Helicotylenchus indicus*; PC = *Paratrichodorus christei*; LA = *Longidorus attenuatus*; AT = *Anguina tritici* J_2 ; HI = *Hoplolaimus indicus*; HG = *Hemicriconemoides mangiferae*. Vertical lines on the bars show \pm SD. Different letters show significant differences between preference (A) and prey accepted and rejected (B). **Prey accepted significantly different from prey rejected. *Prey accepted not significantly different from prey rejected (B). Adapted from Bilgrami et al. (2005).

Dauer juveniles are metabolically active and motile, non-aging but developmentally arrested. Environmental stresses induce formation of the “dauer juvenile” that enhances the tolerance to moisture, temperature, and chemicals extreme conditions. Only predatory diplogasterids – the cutting and sucking type of predators – have such a resting stage. It shares strong similarities with that of entomopathogenic nematodes in being induced when conditions are unfavorable and in possessing enhanced survival abilities. Most other differences remain uncertain, as in sharp contrast to the dauer juveniles of entomopathogenic species, diplogasterids dauers received thus far little attention. It is hypothesized that diplogasterid dauer juveniles possess some degree of tolerance to anhydrobiotic conditions too.

Table 3. Predatory nematodes preference for prey species in choice experiments.

Prey	prey accepted or rejected (%)										
	HM	HO	MI	TM	XA	HL	PC	LA	AT	HI	HG
HM		-16	+04	-16	-48	-56	-32	-52	+04	-84	-88
HO	+16		+24	-12	-44	-32	-28	-04	+12	-72	-76
MI	-04	-24		-16	-44	-52	-28	-40	-16	-84	-88
TM	+16	+12	+16		-12	-28	-08	-08	+28	-76	-80
XA	+48	+44	+44	+12		-24	-12	-08	+40	-56	-60
HL	+56	+28	+52	+28	+24		+12	+28	+56	-44	-36
PC	+32	+28	+28	+16	+12	-12		-16	+44	-44	-40
LA	+52	+04	+40	+08	+08	-28	+16		+48	-36	-32
AT	+04	-12	+16	-28	-40	-56	-44	-48		-92	-88
HI	+84	+72	+84	+76	+44	+44	+44	+36	+92		00
HG	+88	+76	+88	+80	+40	+36	+40	+32	+88	00	

Mean prey accepted or rejected for each species calculated from ten combinations of two prey species. Predator preference = difference in the proportion of two prey species killed in a combination. Proportion of one prey (e.g., HM in a column) killed higher than the other (e.g., HO in a row) in a combination designated as positive (+16%) and referred to as prey accepted, whereas proportion of one prey (e.g., HO in a column) killed less than the other (e.g., HM in a row) in a combination is designated as negative (-16%) and referred to as prey rejected. HM = *Heterodera moths* (juveniles); HO = *Hirschmanniella oryzae*; MI = *Meloidogyne incognita* (juveniles); TM = *Tylenchorhynchus mashhoodi*; XA = *Xiphinema americanum*; HL = *Helicotylenchus indicus*; PC = *Paratrichodorus christei*; LA = *Longidorus attenuatus*; AT = *Anguina tritici* (juveniles); HI = *Hoplolaimus indicus*; HG = *Hemicriconemoides mangiferae*. Adapted from Bilgrami et al. (2005).

2.5. Culture

Efficacy studies largely reflect lack of *in vitro* production methodology (Bilgrami & Brey, 2005). With few exceptions, predators are reared using *in vivo* methods, which require maintaining concurrent prey cultures, thereby greatly reducing efficiency. The ability to mass rear entomopathogenic nematodes was the catalyst driving their

development (Gaugler & Han, 2002). Ease of culture here is due to the ability of entomopathogenic species to feed on symbiotic bacteria, leading ultimately to rearing in 80 000-liter bioreactors (Georgis, 2002).

Table 4. Coefficient of preference for prey nematodes of *Mononchoides gaugleri*.

Prey species	Coefficient of preference ¹	Combinations preferred ²
<i>Meloidogyne incognita</i>	1.00	10
<i>Heterodera moths</i>	0.92	09
<i>Anguina tritici</i>	0.92	09
<i>Hirschmanniella oryzae</i>	0.67	07
<i>Tylenchorhynchus mashhoodi</i>	0.51	06
<i>Xiphinema americanum</i>	0.19	05
<i>Paratrichodorus christei</i>	-0.15	03
<i>Longidorus attenuatus</i>	-0.42	03
<i>Helicotylenchus indicus</i>	-0.57	02
<i>Hoplolaimus indicus</i>	0.00	00
<i>Hemicriconemoides mangiferae</i>	0.00	00

¹Preference is measured on the scale of 0 to +1 for prey accepted and 0 to -1 for prey rejected.

²Number of combinations a prey was killed more than other species. Adapted from Bilgrami et al. (2005).

Diplogasterids can be reared on either prey nematodes or bacteria, both by *in vivo* or *in vitro* methods, since they are facultative and biphasic. *Diplenteron colobocercus*, *B. degressei*, *M. fortidens*, *M. longicaudatus* and *M. gaugleri* have been successfully maintained on *Caenorhabditis*, *Rhabditis*, *Panagrellus*, *Cephalobus*, bacteria or on a combination of nematode and bacteria for multiple generations over a period of several months. In a study on reproductive capacity of *Mononchoides*, cultures with 25 adult female nematodes per 5.5-cm agar Petri dish were started with *E. coli*. After 20 days at 30°C, culture plates averaged an impressive 10 376 individuals. The oviposition rate was 8–10 eggs day⁻¹ female⁻¹ (Siddiqi et al., 2003).

Mononchs possess significant potential to reduce populations of phytoparasitic nematode under field conditions, but they were never considered as a good biocontrol agent. These predators are fastidious to culture due to their localized distribution in field, long life cycles and low rate of fecundity. In contrast, stylet bearing predators appear as better biocontrol agents since they are widely distributed and occur naturally at high densities. However, their long life cycle and culture conditions hinder any practical application. Pillai and Taylor (1968) cultured diplogasterids on a dixenic culture of bacteria and *Aphelenchus avenae*. Prey nematodes and bacteria have supported growth and development of diplogasterid predators, although some appeared to provide better nematode reproduction than others.

2.6. Conservation

Predatory nematode conservation under natural conditions could make their practical utilization possible (Bilgrami & Brey, 2005). As compared to insects and other beneficial predatory nematodes, conservation is simple and cost-effective. Their population and predatory activities may be stimulated to counter parasitic nematode populations in the field. More studies are needed to develop methods for predatory nematodes conservation under natural habitats.

Neem (*Azadirachta indica*) products e.g., leaf powder, sawdust and oilseed cake, used as organic amendments, showed encouraging results in maintaining and conserving predatory nematode densities in the field (Akhtar, 1995; Akhtar & Mahmood, 1993). Mulching may be another option to improve conservation of predatory nematodes in the field. Mulching was found effective in stabilizing a *Iotonchus tenuicaudatus* population feeding on *Tylenchulus semipenetrans* and *Helicotylenchus dihystrera* in orange orchards (Rama & Dasgupta, 1998). More studies are needed on the role of organic soil amendments and nitrogenous compounds in predatory nematode conservation.

3. BIOLOGICAL CONTROL POTENTIALS

Predatory nematodes belong to the Orders Mononchida, Diplogasterida, Rhabditida, Aphelenchida and super families, Dorylaimoidea, Nygolaimoidea, Actinolaimoidea and families Ironidae, Oncholaimidae, Monohysteridae and Thalassogeneridae etc. They show different types of feeding apparatus, and modes of prey searching, catching and feeding mechanisms. Predators of the order Mononchida possess a well developed buccal cavity with strong buccal musculature, tooth, teeth and denticles. They are commonly known as mononchs which feed by cutting, sucking and engulfing an intact prey (e.g., *Mononchus*, *Mylonchulus*, *Iotonchus* etc.) (Bilgrami et al., 1986; Jairajpuri & Bilgrami, 1990). As a result of their inability to perceive prey secretions, their contacts with prey depend on chance encounters. Species belonging to Aphelenchida, Dorylaimoidea and Nygolaimoidea are commonly known as aphelench, dorylaim and nygolaim predators.

Feeding apparatus in dorylaim predators (e.g., *Mesodorylaimus*) is a stylet provided with a lumen. Nygolaim predators (e.g., *Aquatides*) have a feeding apparatus called mural tooth, which is solid. Aphelench predators (e.g. *Seinura*) are provided with a pointed stylet with a lumen for ingestion. Feeding in aphelench, dorylaim and nygolaim predators is piercing and sucking type. Members belonging to Diplogasterida are commonly referred to as diplogasterid predators (e.g., *Mononchoides*) and possess a strong buccal cavity with dorsal movable tooth. Their feeding apparatus is cutting and sucking type. Other nematode groups e.g., pelagonematids, actinolaimids, ironids, monohysterids and enoplids also include predatory species which possess cutting, sucking or piercing types of feeding. However, little is known about predation abilities and role in nematode management.

Predatory nematodes like *Seinura paynei* have been recovered from mushroom substrates feeding on free living nematodes e.g., *Acrobeloides* and *Bursilla* (Grewal, Siddiqi, & Atkey, 1991). The widespread distribution of *Seinura* and their feeding

on nematodes in mushroom substrates suggest that these predators may also control populations of *Aphelenchoides*, parasitic on mushrooms (Grewal et al., 1991). However, more studies are needed to understand true predatory potential of aphelenchid species.

3.1. Biocontrol Potential of Mononchs

Prospects for use of mononchs to control plant-parasitic nematodes were speculated by Cobb (1917; 1920) and Steiner and Henley (1922). Thorne (1927) thought otherwise, considering mononchs unable to control nematode populations. Cassidy (1931), however, reported partial control under suitable conditions using *Iotonchus brachylaimus* as predator.

Further studies were made by Mulvey (1961), Esser (1963) and Ritter and Laumond (1975). Mononchs feed on a variety of soil microorganisms including nematodes (Table 5). According to Webster (1972) and Jones (1974) non-specific predators like mononchs exert only partial control and the possibility of these being successful agents of biological control are remote.

Table 5. List of plant-parasitic nematodes recorded as preys of mononchs.

Predators	Prey nematodes	References
<i>Anatonchus amiciae</i>	<i>Tylenchus</i> , <i>Xiphinema</i>	Coomans and Lima (1965)
<i>A. ginglymodontus</i>	<i>Meloidogyne hapla</i> (juv.)	Szczygiel (1966; 1971)
<i>A. tridentatus</i>	<i>Paratylenchus macrophallus</i> , <i>Aphelenchus</i> , <i>Longidorus</i> , <i>Pratylenchus</i>	Mulvey (1961), Banage (1963)
<i>Clarkus mulveyi</i>	<i>Tylenchorhynchus nudus</i> , <i>Helicotylenchus multincinctus</i> , <i>Rotylenchulus reniformis</i> , <i>M. incognita</i> (juv.).	Mohandas and Prabhoo (1980)
<i>C. papillatus</i>	<i>Tylenchus</i> , <i>Tylenchulus semipenetrans</i> , <i>Tylocephalus auriculatus</i> , <i>Heterodera schachtii</i> (juv.), <i>Hemicriconemoides</i> , <i>Aphelenchoides</i> , <i>M. hapla</i> (juv.)	Cobb (1917), Menzel (1920) Steiner and Heinley (1922)
<i>C. sheri</i>	<i>Tylenchorhynchus</i> , <i>Aphelenchus</i>	Bilgrami et al. (1986)
<i>Coomansus indicus</i>	<i>Pratylenchus</i> , <i>Tylenchorhynchus</i> , <i>Hemicriconemoides</i> , <i>Xiphinema</i>	Bilgrami et al. (1986)
<i>Iotonchus acutus</i>	<i>Trichodorus obtusus</i> , <i>R. robustus</i> , <i>Xiphinema americanum</i>	Cobb (1917), Thorne (1932)

<i>I. amphigonius</i>	<i>H. schachtii</i> (juv.)	Thorne (1924)
<i>I. antidontus</i>	<i>Tylenchorhynchus</i>	Bilgrami et al. (1986)
<i>I. basidontus</i>	<i>Tylenchorhynchus</i>	Bilgrami et al. (1986)
<i>I. brachylaimus</i>	<i>Rhadopholus similis</i> , <i>T. semipenetrans</i>	Cassidy (1981), Mankau (1980)
<i>I. indicus</i>	<i>Tylenchorhynchus</i>	Bilgrami et al. (1986)
<i>I. kherai</i>	<i>T. nudus</i> , <i>Hirschmanniella</i> <i>oryzae</i> , <i>H. multincinctus</i> , <i>R. reniformis</i> , <i>Meloidogyne</i> <i>incognita</i> (juv.), <i>Xiphinema</i> <i>elongatum</i>	Mohandas and Prabhoo (1980)
<i>I. longicaudatus</i>	<i>Hoplolaimus</i> , <i>Hirschmanniella</i>	Bilgrami et al. (1986)
<i>I. monhystera</i>	<i>T. nudus</i> , <i>H. oryzae</i> , <i>H.</i> <i>multincinctus</i> , <i>R. reniformis</i> , <i>M. incognita</i> (juv.)	Azmi (1983), Bilgrami et al. (1986)
<i>I. nayari</i>	<i>X. elongatum</i> , <i>H. oryzae</i> , <i>H. multincinctus</i> , <i>R. reniformis</i> , <i>M. incognita</i> (juv.), <i>T. nudus</i>	Mohandas and Prabhoo (1980)
<i>I. parabasidontus</i>	<i>Hirschmanniella</i>	Bilgrami et al. (1986)
<i>I. prabhooi</i>	<i>R. reniformis</i> , <i>M. incognita</i> (juv.)	Mohandas and Prabhoo (1980), (juv.)
<i>I. risoceiae</i>	<i>Pratylenchus</i>	Bilgrami et al. (1986)
<i>I. shafi</i>	<i>Hoplolaimus</i>	Bilgrami et al. (1986)
<i>I. trichuris</i>	<i>Pratylenchus</i> , <i>Hoplolaimus</i> , <i>Tylenchorhynchus</i> , <i>Xiphinema</i>	Bilgrami et al. (1986)
<i>I. vulvapurillatus</i>	<i>Tylenchorhynchus</i>	Andrassy (1964), Andrassy (1973)
<i>Miconchus aquaticus</i>	<i>Helicotylenchus</i> , <i>Xiphinema</i> , <i>Hemicyclophora</i>	Bilgrami et al. (1986)
<i>M. citri</i>	<i>Pratylenchus</i> , <i>Tylenchorhynchus</i>	Bilgrami et al. (1986)
<i>M. dalhousiensis</i>	<i>Aphelenchoides</i>	Bilgrami et al. (1986)
<i>Mononchus aquaticus</i>	<i>Tylenchorhynchus mashoodi</i> , <i>H. oryzae</i> , <i>Hoplolaimus indicus</i> , <i>Helicotylenchus indicus</i> , <i>X. americanum</i> , <i>Longidorus</i> , <i>Paralongidorus citri</i> , <i>Paratrichodorus</i> , <i>Anguina</i> <i>tritici</i> (juv.), <i>M. incognita</i> (juv.), <i>Meloidogyne naasi</i> (juv.), <i>Heterodera mothi</i> (juv.), <i>Rotylenchus fallorobustus</i> , <i>Globodera rostochiensis</i> (juv.)	Grootaert and Maertens (1976), Grootaert et al. (1977), Small and Grootaert (1983), Bilgrami (1992), Bilgrami et al. (1986)
<i>M. truncatus</i>	<i>H. schachtii</i>	Thorne (1927)

(continued)

Table 5 (continued)

<i>Predators</i>	<i>Prey nematodes</i>	<i>References</i>
<i>M. tunbridgensis</i>	<i>Aphelenchus avenae</i> , <i>T. semipetrans</i> , <i>Hoplolaimus</i> , <i>Tylenchorhynchus</i> , <i>Hemicriconemoides</i>	Mankau (1980), Bilgrami et al. (1986)
<i>Mylonchulus agilis</i>	<i>Helicotylenchus vulgaris</i> , <i>R. fallorobustus</i> , <i>Longidorus caespiticola</i>	Doucet (1980)
<i>M. brachyuris</i>	<i>Subanguina radiculicola</i> , <i>R. similis</i>	Cassidy (1931)
<i>M. dentatus</i>	<i>A. avenae</i> , <i>Helicotylenchus indicus</i> , <i>H. indicus</i> , <i>T. mashhoodi</i> , <i>M. incognita</i> (juv.), <i>H. mothi</i> (juv.), <i>H. oryzae</i> , <i>T. semipetrans</i> , <i>Basiria</i> , <i>Xiphinema</i> , <i>Paralongidorus citri</i> , <i>Longidorus</i>	Jairajpuri and Azmi (1978), Bilgrami and Kulshreshtha (1994)
<i>M. hawaiiensis</i>	<i>T. nudus</i> , <i>H. oryzae</i> , <i>R. reniformis</i> <i>M. incognita</i> (juv.)	Mohandas and Prabhoo (1980)
<i>M. minor</i>	<i>A. tritici</i> (juv.), <i>M. incognita</i> (juv), <i>T. semipetrans</i> , <i>X. americanum</i> . <i>R. reniformis</i>	Kulshreshtha, Bilgrami, and Khan (1993), Choudhary and Sivakumar (2000)
<i>M. parabrachuris</i>	<i>H. schachtii</i> (juv)	Thorne (1927)
<i>M. sigmaturus</i>	<i>H. schachtii</i> (juv.), <i>R. similis</i> , <i>T. semipetrans</i> , <i>Meloidogyne javanica</i> (juv.), <i>Subanguina radiculicola</i>	Thorne (1927), Cassidy (1931), Cohn and Mordechai (1973, 1974), Mankau (1982)
<i>Prionchulus muscorum</i>	<i>Aphelenchus</i> , <i>Hoplolaimus</i> , <i>Tylenchorhynchus</i> , <i>Hemicriconemoides</i> , <i>Aphelenchus</i>	Szczygiel (1971), Arpin (1976) Bilgrami et al. (1986)
<i>P. punctatus</i>	<i>A. avenae</i> , <i>M. naasi</i> (juv.) <i>G. rostochiensis</i> (juv.), <i>R. fallorobustus</i> , <i>Helicotylenchus</i> , <i>A. tritici</i> (juv.)	Nelmes (1974), Maertens (1975), Grootaert et al. (1977), Small and Grootaert (1983), Small (1979)
<i>Sporonchulus ibitiensis</i>	<i>Aphelenchus</i> , <i>Aphelenchoides</i>	Carvalho (1951)
<i>S. vagabundus</i>	<i>Aphelenchoides</i> , <i>Hemicycliophora</i> , <i>Trichodorus</i>	Bilgrami et al. (1986)

Predatory nematodes remained neglected until 1974 when Cohn and Mordechai (1974) found correlation between *Mylonchulus* and *Tylenchulus* in pot experiments. Similarly, Small (1979) reported significant reduction in *Globodera* and *Meloidogyne* populations in the presence of *Prionchulus*. Ahmad and Jairajpuri (1982) reported significant correlation between *Parahadronchus* and *Trichodorus*

and *Hemicriconemoides* under field conditions. Azmi (1983) indicated increase in *Iotonchus* and reduction in *Helicotylenchus* populations.

Observations on the predation by mononchs viz., factors influencing predation (Bilgrami, Ahmad, & Jairajpuri, 1983); predation (Nelmes, 1974; Small & Grootaert, 1983; Bilgrami, Ahmad, & Jairajpuri, 1984; Kulshreshtha et al., 1993; Bilgrami et al., 1986); predator strike rate, prey resistance and susceptibility to predation (Bilgrami & Jairajpuri, 1989a; Bilgrami, 1992, 1995); relationships with prey trophic groups (Bilgrami, 1992); cannibalism (Bilgrami & Jairajpuri, 1984); and range of prey (Small, 1979, 1987) etc., were made to evaluate predatory potential of mononchs. In a study by Bilgrami et al. (1986) analysis of gut contents of mononchs revealed their voracious feeding on different species of plant-parasitic nematodes. Dorylaim, tylench and bacteriophagous nematodes were found intact within the intestine, while others were present in semi digested conditions (Table 2).

Under natural conditions mononchs feed upon all types of nematodes, besides rotifers and other soil microorganisms. Arpin (1979) and Mahapatra and Rao (1980) found significant correlation between mononchs and free-living but Nelmes and McCulloch (1975) did not find such a correlation. Study made by Bilgrami et al., (1986) showed that more predators (75%) had free-living nematodes in their intestine than tylenchs (45%) or dorylaims (41%) (Table 2).

Any relationship of mononchs with prey nematodes present in the soil could not be determined since observations were made on mounted specimens and not the live populations. It cannot be suggested with certainty that widespread presence of free-living nematodes is either due to any preference or due to the widespread occurrence of free-living nematodes. Of all the mononchs, *Parahadronchus* was the most active predator as 68% of its specimens had prey in its intestine while *Coomansus* was least active with only 21% prey. Eight genera of Tylenchida, six of Dorylaimida, five of Mononchida, three of Rhabditida and one each of Diplogasterida and Monhystera were identified as prey of *Parahadronchus shakily*. Mohandas and Prabhoo (1980) did not find any prey in the intestine of *Mylonchulus* spp.

3.2. Biocontrol Potential of Dorylaim and Nygolaim Predators

Dorylaim, nygolaim and aphelench predators, which have piercing-sucking type of feeding (Bilgrami & Gaugler, 2004), can switch to feeding on bacteria and fungi (Hollis, 1957; Ferris, 1968; Wood, 1973), which presumably enhances their survival when prey nematodes are scarce.

In addition to nematodes (Wyss & Grootaert, 1977; Shafqat et al., 1987; Khan et al., 1991), dorylaim and nygolaim predators also feed on algae and fungi (Hollis, 1957; Ferris, 1968; Wood, 1973; Bilgrami, 1990b) (Table 6). Consequently, they can also be grown on algae and fungi. Their widespread and abundant presence reflects the possibility of controlling nematode populations. It is, however, not known up to what extent and under what conditions nematode populations are reduced, since such an evaluation has never been made. Dorylaim and nygolaim

predators occur in all soil types, climates and habitats. The presence of 2, 3 or more genera at one field/place is quite common.

Feeding of *Eudorylaimus obtusicaudatus* on *Heterodera schachtii* eggs and increased population of *Thornia* sp., in the presence of citrus nematode suggests their control potential. *Aporcelaimellus*, *Discolaimus*, *Mesodorylaimus* and *Dorylaimus* (Khan et al., 1991; Khan, Bilgrami, & Jairajpuri, 1995a; Khan, Bilgrami, & Jairajpuri, 1995b; Bilgrami, 1992, 1993, 1995) showed significant predatory potential. They are attracted towards prey and aggregate at the feeding sites in response to prey secretions. Predation rate, feeding, aggregation, and prey search activities are governed by biotic and abiotic factors such as temperature, density, starvation, incubation, etc. These factors affect their chemotactic responses (Bilgrami & Jairajpuri, 1988a), dispersion of prey kairomones (Green, 1980) and rate of predation (Bilgrami, 1997). Reduced predator activity (Bilgrami et al. 1983) and depleted prey attractants (Huettel, 1986) as influenced by temperature extremes are also possible causes of reduced predation.

Similarly to temperature, predatory activities are also affected by starvation (Jairajpuri & Bilgrami, 1990). Starvation of 14 days did not alter predation by *Dorylaimus stagnalis* (Bilgrami et al., 1984; Shafqat et al., 1987) but short-term food deprivation enhanced predation. Bilgrami and Gaugler (2005) observed maximal predation in 6 days starved predators, presumably because food deprivations increased predator ability to detect more prey individuals to kill. Doncaster and Seymour (1974) concluded that starved nematodes could perceive weaker stimuli much faster than when they are well fed, because of decreased minimum response threshold. Stylet bearing predators show density dependent predation (Khan et al., 1991) similar to other group of predators. More predator-prey encounters at higher prey densities always result in the increased rate of predation.

Table 6. Plant-parasitic nematodes as prey of dorylaim, nygolaim and tylenchid predators.

Predators	Prey nematodes	References
<i>Allodorylaimus americanus</i>	<i>M. incognita</i> (juv.), <i>A. tritici</i> (juv.), <i>Xiphinema basiri</i> , <i>Longidorus</i> , <i>T. mashoodi</i> , <i>H. oryzae</i> , <i>Aphelenchoides</i> , <i>Basiria</i> , <i>A. avenae</i> , <i>T. semipenetrans</i> , <i>Trichodorus</i>	Khan et al. (1995a, 1995b)
<i>A. amylovorus</i> <i>A. obscurus</i>	<i>T. semipenetrans</i> <i>H. schachtii</i> (juv.)	Mankau (1982) Thorne and Swanger (1936)
<i>A. obtusicaudatus</i>	<i>H. schachtii</i> (juv.)	Marinari, Vinciguerra, Vovlas and Zullini (1982)
<i>A. nivalis</i>	<i>M. incognita</i> (juv.), <i>H. moths</i> (juv.), <i>X. basiri</i> , <i>Longidorus</i> , <i>T. mashoodi</i> , <i>H. oryzae</i> , <i>H. indicus</i> , <i>Aphelenchoides</i> , <i>Basiria</i> , <i>A. avenae</i> , <i>T. semipenetrans</i> , <i>Trichodorus</i>	Bilgrami (1993), Khan et al. (1991)
<i>Discolaimus arenicolus</i>	<i>M. incognita</i> (juv.)	Yeates et al. (1993)

<i>D. silvicolus</i>	<i>M. incognita</i> (juv.), <i>H. mothi</i> (juv.), <i>A. tritici</i> (juv.), <i>X. basiri</i> , <i>Longidorus</i> , <i>T. mashoodi</i> , <i>H. oryzae</i> , <i>Aphelenchoides</i> , <i>Basiria</i> , <i>A. avenae</i> , <i>T. semipenetrans</i> , <i>Trichodorus</i>	Khan et al. (1995a)
<i>Dorylaimus obtusicaudatus</i>	<i>H. schachtii</i> (eggs)	Cobb (1929)
<i>D. obscurus</i>	<i>H. schachtii</i> (eggs)	Thorne and Swanger (1936)
<i>D. stagnalis</i>	<i>T. mashoodi</i> , <i>H. oryzae</i> , <i>H. indicus</i> <i>X. americanum</i> , <i>Longidorus</i> , <i>P. citri</i> , <i>A. tritici</i> (Juv.), <i>M. incognita</i> (juv.) <i>H. mothi</i> (juv.)	Bilgrami (1992) Shafqat et al. (1987)
<i>Eudorylaimus obtusicaudatus</i>	<i>H. schachtii</i>	Esser (1987)
<i>Labronema vulvapapillatum</i>	<i>A. avenae</i> , <i>A. tritici</i> (juv.) <i>M. naasi</i> (juv.), <i>G. rostochiensis</i> (juv.)	Wyss and Grootaert (1977) Grootaert and Small (1982), Small and Grootaert (1983), Esser (1987)
<i>Mesodorylaimus bastiani</i>	<i>M. incognita</i> (juv.), <i>H. mothi</i> (juv.) <i>X. basiri</i> , <i>X. americanum</i> , <i>X. insigne</i> , <i>Longidorus</i> , <i>T. mashoodi</i> , <i>H. oryzae</i> , <i>H. indicus</i> , <i>Aphelenchoides</i> , <i>Basiria</i> , <i>A. avenae</i> , <i>T. semipenetrans</i> , <i>Trichodorus</i> , <i>Paratrichodorus</i> , <i>A. tritici</i> (juv.), <i>Longidorus</i> , <i>T. mashoodi</i>	Bilgrami (1992)
<i>Pungentus monohystera</i>	<i>T. semipenetrans</i>	Mankau (1982)
<i>Seimura celeris</i>	<i>A. avenae</i>	Hechler and Taylor (1966)
<i>S. demani</i>	<i>A. bicaudatus</i> , <i>A. avenae</i>	Wood (1974)
<i>S. oliveirae</i>	<i>A. avenae</i>	Hechler and Taylor (1966)
<i>S. oxura</i>	<i>A. avenae</i> , <i>Ditylenchus myceliophagus</i>	Hechler and Taylor (1966), Cayrol (1970)
<i>S. steineri</i>	<i>A. avenae</i>	Hechler and Taylor (1966)
<i>S. tenuicaudata</i>	<i>M. marioni</i> (juv.), <i>Pratylenchus pratensis</i> <i>A. avenae</i> , <i>A. parietinus</i> <i>D. dipsaci</i> , <i>Heterodera trifolii</i> (juv.), <i>M. hapla</i> (juv.), <i>Neotylenchus linfordi</i>	Linford and Oliviera (1937), Hechler (1963)

(continued)

3.3. Biocontrol Potential of Diplogasterid Predators

Diplogasterid predators remained largely neglected until Yeates (1969) evaluated predatory abilities of *Diplenteron*. Subsequent studies (Goodrich, Hechler, & Taylor, 1969; Grootaert et al., 1977) brought to light more information on their biology, behaviour, predator-prey relationships, ecology, predation abilities etc. Despite these efforts, diplogasterid predators have received thus far less attention (Bilgrami & Jairajpuri, 1989a; Fauzia, Jairajpuri, & Khan, 1998) (Table 7) than the large and easily studied mononchs, yet they possess more favorable biological control traits.

Bilgrami and Jairajpuri (1988a, 1989a, 1989b) and Bilgrami (1990a, 1997) made the first case for diplogasterid predators by offering detailed accounts on their prey searching, preference, strike rate, and prey resistance and susceptibility to predation. Among the advantages of diplogasterids over mononch predators, these authors listed ease of *in vitro* culture, high rates of reproduction and predation, short life cycle, ability to detect and respond to prey attractants, and rare cannibalism. Diplogasterids further differ from mononch juveniles in possessing greater tolerance to unfavourable environmental conditions (Bilgrami, 1997).

Particularly significant were the observations of Yeates (1969), Grootaert et al., (1977) and Bilgrami (1997) that the diplogasterids *Diplenteron* and *Butlerius* switch to feeding on bacteria in the absence of prey, strongly suggesting an enhanced capability to persist when prey populations are reduced. Switching food resources is therefore a common trait among predaceous diplogasterids. Fauzia et al. (1998) subsequently demonstrated the ability of *Mononchoides* to reduce galling by root knot nematodes in post tests, resulting in improved vegetative growth and increased root mass.

Recently, Bilgrami, Brey, and Gaugler (2007) made first field release of a diplogasterid predator *Mononchoides gaugleri* to determine its effect on existing parasitic nematode populations in a turf grass fields. They reported significant control of plant-parasitic nematodes although the rate of predator persistence was low.

Prey preference is another desirable feature in biological control agents but predators, whether mammalian, reptilian, insect, or nematode, tend to be polyphagous. Mononchs, too, are polyphagous (Bilgrami et al., 1984; Bilgrami 1997). However, diplogasterid predators appear to be more prey-specific as indicated by *Odontopharynx* which attacked and killed six of 17 species presented in a laboratory study (Chitambar & Noffsinger, 1989). Moreover, some prey species were preferred more strongly than others. A strong degree of preference was similarly reported for other diplogasterid predators *Butlerius* and *Mononchoides*. Bilgrami and Jairajpuri (1989a) and Bilgrami et al. (2005) showed that *M. longicaudatus*, *M. fortidens* and *M. gaugleri* preferred endoparasitic over ectoparasitic prey species.

Table 7. List of plant-parasitic nematodes recorded as prey of diplogasterid predators.

	<i>Prey nematodes</i>	<i>References</i>
<i>Butlerius degrissei</i>	<i>A. avenae</i> , <i>A. fragariae</i>	Grootaert et al. (1977)
	<i>Pratylenchus</i> , <i>G. rostochiensis</i> (juveniles)	Grootaert and Jaques (1979)
	<i>R. robustus</i>	Small and Grootaert (1983)
<i>B. micans</i>	<i>A. avenae</i>	Pillai and Taylor (1968)
<i>Fictor anchicoprophaga</i>	<i>A. avenae</i>	Pillai and Taylor (1968)
<i>Mononchoides bollingeri</i>	<i>A. avenae</i>	Goodrich et al. (1968)
<i>M. changi</i>	<i>A. avenae</i>	Goodrich et al. (1968)
<i>M. fortidens</i>	<i>M. incognita</i> (juv.), <i>A. tritici</i> (juv.)	Bilgrami and Jairajpuri (1988, 1989)
	<i>T. mashoodi</i> , <i>X. americanum</i> , <i>H. indicus</i> , <i>Longidorus</i> , <i>Trichodorus</i>	
<i>M. gaugleri</i>	<i>M. incognita</i> (juv.), <i>A. tritici</i> (juv.), <i>H. mothi</i> (juv), <i>T. mashoodi</i> , <i>Longidorus</i> , <i>X. americanum</i> , <i>Trichodorus</i>	Bilgrami et al. (2005)
	<i>H. indicus</i> , <i>H. mangiferae</i> , <i>P. christei</i>	
<i>M. longicaudatus</i>	<i>M. incognita</i> (juv.), <i>A. tritici</i> (juv.)	Bilgrami and Jairajpuri (1988b, 1989)
	<i>T. mashoodi</i> , <i>X. americanum</i> , <i>H. indicus</i> , <i>Longidorus</i> , <i>Trichodorus</i>	

4. FUTURE PROSPECTS

Predatory nematodes represent a small amount of the available biomass in the soil, but their presence across so many trophic levels e.g., plant, fungal, bacterial and carrion feeders is vitally important in soil ecosystem processes (Barker & Koenning, 1998). Their future role in nematode management depends greatly on advances made on other control methods, their effectiveness, and the resources provided to establish research programs.

The real possibility of using predatory nematodes in nematode management programs lies in the diplogasterid predators due to their biphasic feeding, high rates of predation and fecundity, short life cycle, ability to search for prey and the presence of resistant juveniles. Diplogasterid predators rarely resort to cannibalism due to their bacteriophagous feeding habits.

Despite remarkable similarities with the attributes of entomopathogenic nematode species, diplogasterids should not be considered as unilateral inundative agents (i.e., repeated applications for short-term control). The flexible bi-phasic feeding behaviour of diplogasterids should endow them with superior persistence; that is, when prey become scarce they should switch to feeding on soil bacteria to maintain themselves. Nematode predators are likely to offer the most promise as augmentative agents in colonization efforts in combination with cultural control tactics, such as rotation, cover cropping, green manuring, organic amendments.

Dorylaim and nygolaim predators are ubiquitous species, occurring in all types of climates and habitats. The presence of two, three or more genera of dorylaims and nygolaims at one field/place is quite usual and their abundance has been estimated to be 200–500 millions/acre (Thorne, 1930). Their widespread and abundant presence, the omnivorous feeding habits, the ability to perceive prey kairomones, and the inverse relationships with prey populations observed in pot trails (Boosalis & Mankau, 1965) indicate their potential as nematode biological control agents.

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