Resistance of prey to predation and strike rate of the predators, *Mononchoides longicaudatus* and *M. fortidens* (Nematoda : Diplogasterida)

Anwar L. BILGRAMI and M. Shamim JAIRAJPURI

Section of Nematology, Department of Zoology, Aligarh Muslim University, Aligarh-202002, India.

SUMMARY

Resistance of prey nematodes to predation, strike rate of the predators, *Mononchoides longicaudatus* and *M. fortidens* and their ability to wound prey and feed upon them was determined on agar plates. *M. longicaudatus* and *M. fortidens* attacked all kinds of prey nematodes. The second stage juveniles of *Meloidogyne incognita* and *Anguina tritici* and the adult *Acrobeloides* sp., *Cephalobus* sp., and *Panagrellus redivivus* were most susceptible to predation while *Hemicriconemoides mangiferae* and *Hoplolaimus indicus* were totally resistant. *Hirschmanniella oryzae, Helicotylenchus indicus, Tylenchorhynchus mashhoodi, Xiphinema americanum, Rhabditis* sp., *Trichodorus* sp., and *Longidorus* sp., were attacked with intermediate frequencies. *M. longicaudatus* took a minimum of 15-25 min. to finish a juvenile of *M. incognita* and maximum 80-110 min. for the *Longidorus* sp., white *M. fortidens* consistently consumed prey at a faster rate.

RÉSUMÉ

Résistance des proies à la prédation et taux d'attaque des prédateurs Mononchoides longicaudatus *et* M. fortidens *(Nematoda : Diplogasterida)*

La résistance des nématodes-proies à la prédation, le taux d'attaque des prédateurs, *Mononchoides longicaudatus* et *M. fortidens,* ainsi que leur habileté à blesser les proies et s'en nourrir ont été déterminés sur plaques de gélose. *M. longicaudatus* et *M. fortidens* attaquent tous les types de proies. Les juvéniles de deuxième stade de *Meloigyne incognita* et d'*Anguina tritici* et les adultes d'*Acrobeloides* sp. *Cephalobus* sp. et *Panagrellus redivivus* sont les plus exposés à la prédation tandis que *Hemicriconemoides mangiferae* et *Hoplolaimus indicus* sont totalement résistants. *Hirschmanniella oryzae, Helicotylenchus indicus, Tylenchorhynchus mashhoodi, Xiphinema americanum, Rhabditis* sp., *Trichodorus* sp. et *Longidorus* sp. sont attaqués avec des fréquences moyennes. Il faut à *M. longicaudatus* un minimum de 15 à 25 minutes pour achever un juvénile de *M. incognita,* et un maximum de 80-110 minutes pour *Longidorus* sp., tandis que *M. fortidens* ingère ses proies plus rapidement.

The predatory nematodes use a variety of mechanisms to obtain prey. Similarly, prey nematodes possess certain qualities such as the thick cuticle, annulations, chemical secretions, etc., which may protect them from predators (Esser, 1963). Esser (1963) provided a list of nematodes that he found to be susceptible or resistant to predation by different mononchs and dorylaims. Grootaert, Jaques and Small (1977) observed prey selection in *Butlerius* sp., and measured susceptibility and resistance to predation of tylenchid, aerolaimid, enoplid and dorylaimid nematodes. Small and Grootaert (1983) described anti-predation adaptations in prey nematodes. Very recently, Shafqat, Bilgrami and Jairajpuri (1987) observed prey selection in *Dorylaimus stagnalis* Dujardin, 1845 and suggested that the thick cuticle of *Hoplolaimus indicus* Sher, 1963 and chemical secretions of *Helicotylenchus indicus* Siddiqi, 1963 may represent anti-predation devices.

The present work describes experiments conducted to determine the degree of resistance/susceptibility of different plant-parasitic and free-living nematodes to predation by *Mononchoides longicaudatus* (Khera, 1965) Andrássy, 1984 and *M. fortidens* (Schuurmans Stekhoven, 1951) Taylor & Hechler, 1966.

Materials and methods

M. fortidens and *M. longicaudatus* were cultured by the methods of Bilgrami and Jairajpuri (1988). Adult *Acrobeloides* sp., *Cephalobus* sp., *Rhabditis* sp., *Panagrellus redivivus, Trichodorus* sp., *Longidorus* sp., *Xiphinema americanum, Hirschmanniella oryzae, Tylenchorhynchus mashhoodi, Hoplolaimus indicus, Helicotylenchus indicus, Hemicriconemoides mangiferae* and the second stage juveniles of *Meloidogyne incognita* and *Anguina tritici* were used as prey.

The free-living nematodes were obtained from the cultures maintained in the laboratory. These prey nematodes were cultured in Petri dishes containing 1 % water-agar. 5 mg of infant milk powder (Lactogen®) was spread over the surface of agar to grow bacteria which served as food for the prey nematodes. The second stage juveniles of *M. incognita* and *A. tritici* were obtained from population maintained on tomato and the wheat galls respectively. Other prey nematodes were isolated fresh from soil for each experiment. 500 g of soil containing nematodes was processed by decantation and Baermann's funnel techniques.

The encounters (lip contact of predator with the prey at right angle) between predators and prey were observed in Petri dishes containing 1 % water-agar using a stereoscopic binocular microscope. For each encounter a new predator and a prey individual was used (irrespective of whether the predator failed or succeeded in attacking the prey). A prey nematode was placed in front of the head of an active predator with the help of a fine needle without touching (disturbing) the predator in any manner. Only those observations were recorded where the predators behaved as normally as could be ensured. To reduce the effects of satiation and prey habituation, 4-6 day starved adult predators were tested. Fifty encounters were observed between predator and prey.

The strike rate of predator may be defined as the percentage of success with which it attacks prey (attack represents the rapid movement of head and the application of suction created by oesophagous of the predator) and may reflect its predatory potential. The strike rate *(SR)* of *M. longicaudatus* and *M. fortidens* could be determined by the followiing formula :

$$SR\ (\%) = \frac{EA}{E} \times 100$$

Where EA = total number of encounters resulting into attack; E = total number of encounters made by the predator.

The resistance of a prey may be defined as the degree of their ability to avoid predation (wounding) by physical, chemical or behavioural means. The percentage degree of resistance of a prey may be calculated as follows :

$$PR\ (\%) = \frac{EA - AW}{EA} \times 100$$

Where PR = prey resistance; AW = total number of attacks resulting into prey wounding.

The susceptibility of a prey may be defined as their degree of succumbing to predation (wounding). The percent susceptibility of prey to predation may thus be obtained by the following formula :

$(PS\ (\%) = 100 - PR$ (PS = prey susceptibility)

During the present study the wounding was considered as the primary factor in measuring prey resistance/susceptibility since it is an important factor in predation (Small & Grootaert, 1983). Esser (1987) also suggested that resistance of a prey is lost if it is wounded or is in a weakened condition. A wound may result in the loss of hydrostatic pressure of the body affecting locomotion and thereby making the prey more vulnerable to predation. Wounding may also permit invasion of pathogenic micro-organisms resulting into the death of prey. The mere encounters between the predator and the prey may not necessarily result into wounding of the prey.

The percentage of predators which started feeding after wounding the prey and the percentage of prey which were left unfinished by the predators were also determined. Both species of predators were tested separately. The untransformed results were analysed to obtain correlation coefficients (" r "), standard error *(SE)* and level of significance (" P ") with the help of the following statistical tests :

$$\text{Correlation coefficient (" } r \text{ ")} = \frac{\Sigma XY}{\sqrt{\Sigma X^2 \, \Sigma Y^2}}$$

$$\text{Standard error } (SE \pm) = \frac{1 - r^2}{\sqrt{N}}$$

Where X and Y are the deviations measured from their respective means and N is the number of replicates. Significance of " r " values was obtained directly from the Table for the significance of the Correlation coefficient.

Results

The results show a high degree of correlation between the two species of predators for encounters resulting into attack ($r = 0.89$, $SE \pm 0.05$, $p < 0.05$); attacks resulting into wounding ($r = 0.98$, $SE \pm 0.01$, $p < 0.05$); feeding after wounding ($r = 0.98$, $SE \pm 0.01$, $p < 0.05$) and number of prey left unfinished ($r = 0.83$, $SE \pm 0.05$, $p < 0.05$).

Resistance of prey to predation and strike rate of *M. longicaudatus*

M. longicaudatus attacked all types of prey nematodes with lowest strike rate on *H. mangiferae* (46 %). Encounters with *P. redivivus*, *Acrobeloides* sp., *Cephalobus* sp., and the second stage juveniles of *M. incognita* and *A. tritici* resulted in maximum strike rate (92-96 %) and prey wounding (95-100 %) by *M. longicaudatus* (Tab. 1). The success of *M. longicaudatus* in attacking other prey species ranged between 68-90 %. This predator did not succeed in wounding any individual belonging to *Hoplolaimus indicus* or *H. mangiferae* but attacked 74 % and

Table 1

Resistance of prey to predation and strike rate of *Mononchoides longicaudatus*

Prey nematodes	*Number of encounters*	*Number of encounters resulting into attack*	*Strike rate of predator*	*Number of attacks resulting in pray wounding*	*Degree of resistance susceptibility*		*Feeding after wounding prey*	*Prey left unfinished*	*Duration of feeding on single prey*
	(E)	*(EA)*	*SR (%)*	*AW——*	*PR (%)*	*PS (%)*	*(%)*	*(%)*	*(mn)*
Panagrellus redivivus	50	47	94	46	4	96	100	0	30-35
Acrobeloides sp.	50	48	96	48	0	100	96	0	20-25
Cephalobus sp.	50	48	96	48	0	100	100	6	20-25
Rhabditis sp.	50	45	90	29	36	64	86	16	30-45
Anguina tritici juv.	50	46	92	43	7	93	98	10	25-30
Meloidogyne incognita juv.	50	48	96	46	4	96	98	7	15-25
Hirschmanniella oryzae	50	43	86	35	19	81	94	30	40-55
Tylenchorhynchus mashhoodi	50	42	84	33	21	79	73	25	35-50
Helicotylenchus indicus	50	34	68	25	26	74	48	58	60-70
Longidorus sp.	50	36	72	22	39	61	56	50	80-110
Xiphinema americanum	50	34	68	22	35	65	45	50	70-85
Hoplolaimus indicus	50	37	74	0	0	0	0	0	0
Hemicriconemoides mangiferae	50	23	46	0	0	0	0	0	0
Trichodorus sp.	50	39	78	22	44	56	77	47	45-60

All figures are nearest to whole numbers.

46 % of the individuals respectively. The second stages of *M. incognita* and *A. tritici* along with the adult *Acrobeloides* sp., *P. redivivus* and *Cephalobus* sp., were highly susceptible to predation having only 0-6 % resistance against *M. longicaudatus* (Tab. 1). Other prey nematodes viz., *H. oryzae*, *T. mashhoodi*, *Helicotylenchus indicus*, *X. americanum*, *Rhabditis* sp., *Trichodorus* sp., and *Longidorus* sp., had low to moderate degree of resistance against predation. The percentage of predators which continued feeding on the prey after wounding them was also highest for the most susceptible prey nematodes as mentioned above. The percentage of predators feeding on *Rhabditis* sp., was also high (86 %) although this species was not wounded as frequently as the most susceptible prey species. In contrast, fewer *M. longicaudatus* (27 %) continued feeding after wounding 74 % *Helicotylenchus indicus*. When feeding occurred no individual of *P. redivivus* and *Acrobeloides* sp., was left unfinished by *M. longicaudatus* while 58 % of *Helicotylenchus indicus*, 50 % *X. americanum* and 50 % *Longidorus* sp., were not completely consumed ($p < 0.05$). *M. longicaudatus* took 15-25 min to finish a *M. incognita* juvenile but 80-110 min for *Longidorus* sp.

Resistance of prey to predation and strike rate of *M. fortidens*

Though *M. fortidens* attacked *Hoplolaimus indicus* and *H. mangiferae* at success rates of 66 % and 56 % respectively, but none of them were ever wounded. Maximum strike rates occurred against *P. redivivus*, *Acrobeloides* sp., *Cephalobus* sp., and the second stage juveniles of *M. incognita* and *A. tritici* (96-100 %). These nematodes were highly susceptible to predation (*PR* = 0-2 %). Consumption of these prey was also high (96-100 %) (Tab. 2). Least number of attacks by *M. fortidens* resulted into wounding *X. americanum* and *Longidorus* sp., as with *M. longicaudatus*. Few attacks by *M. fortidens* resulted in wounding *Rhabditis* sp., but wounded animals were usually consumed. In contrast, only 51 % of the predators fed on 78 % of *Helicotylenchus indicus* which were wounded and 56 % of these individuals were not completely consumed. No individuals of *P. redivivus* and *Acrobeloides* sp., were left unfinished by the predators. *M. fortidens* required 15-20 min to consume a *M. incognita* juvenile *Acrobeloides* sp., and *Cephalobus* sp., and 60-80 min to consume a *Longidorus* sp., (Tab. 2).

Table 2

Resistance of prey to predation and strike rate of *Mononchoides fortidens*

Prey nematodes	*Number of encounters*	*Number of encounters resulting into attack*	*Strike rate of predator*	*Number of attacks resulting in prey wounding*	*Degree of resistance susceptibility*		*Feeding after wounding prey*	*Prey left unfinished*	*Duration of feeding on single prey*
	(E)	*(EA)*	*SR (%)*	*AW——*	*PR (%)*	*PS (%)*	*(%)*	*(%)*	*(mn)*
Panagrellus redivivus	50	49	98	49	0	100	99	0	20-25
Acrobeloides sp.	50	48	96	47	2	98	100	0	15-20
Cephalobus sp.	50	50	100	50	0	100	100	4	15-20
Rhabditis sp.	50	48	96	34	29	71	88	13	25-35
Anguina tritici juv.	50	48	96	47	2	98	96	4	15-25
Meloidogyne incognita juv.	50	50	100	49	2	98	100	2	15-20
Hirschmanniella oryzae	50	44	88	37	16	84	89	18	30-40
Tylenchorhynchus mashhoodi	50	44	88	39	11	89	77	20	35-40
Helicotylenchus indicus	50	45	90	35	22	78	51	56	50-55
Longidorus sp.	50	39	78	30	23	77	67	50	60-70
Xiphinema americanum	50	40	80	33	18	82	61	45	40-55
Hoplolaimus indicus	50	33	66	0	0	0	0	0	0
Hemicriconemoides mangiferae	50	28	56	0	0	0	0	0	0
Trichodorus sp.	50	42	84	25	40	60	80	40	35-45

All figures are nearest to whole numbers.

Discussion

The high degree of correlation between *M. fortidens* and *M. longicaudatus* for encounters resulting into attack, attacks resulting in prey wounding, feeding after wounding and number of prey left unconsumed indicates that both species of predators are very similar in their behaviour and requirements and also that the predator-prey relationship measured for one species of predator strongly supports the observations made with other predator.

The prey nematodes can resist predation by physical, chemical and behavioural characteristics (Esser, 1963, 1987; Esser & Sobers, 1964) such as thick cuticles (Esser, 1963; Small & Grootaert, 1983); annulations (Esser, 1963); speed (Esser, 1963; Bilgrami, Ahmed & Jairajpuri, 1983); vigorous escape response (Grootaert, Jaques & Small, 1977; Small & Grootaert, 1983); toxic/unfavourable chemical secretions (Esser, 1963). Lack of predation, during the present experiments, on *Hoplolaimus indicus* and *H. mangiferae* might have resulted from their thick cuticles and annulations respectively, that provided resistance to prey from wounding. *Mylonchulus dentatus* and *Dorylaimus stagnalis* also failed to kill or injure *Hoplolaimus indicus* (Jairajpuri & Azmi, 1978; Shafqat, Bilgrami & Jairajpuri, 1987). These authors also attributed thick cuticle as an anti-predation characteristic. Small and Grootaert (1983) attributed active body undulations and vigorous escape response of *Rhabditis oxycerca*, *Pelodera* sp., and *Plectus* sp., as characteristics providing resistance against predation. During present study a combination of high attack rate against *Rhabditis* sp., comparatively lower rate of wounding and higher rate of feeding upon wounded individuals suggests that this prey nematode also relies primarily on active body undulations and vigorous escape response movements to resist predation by *M. longicaudatus* and *M. fortidens.*

The high degree of susceptibility to predation of *Cephalobus* sp., *Acrobeloides* sp., *P. redivivus* along with the second stage juveniles of *M. incognita* and *A. tritici* may be due to small body size, slow rate of movement and lack of protective cuticle adaptations (Bilgrami, Ahmad & Jairajpuri, 1983). These characteristics may be common among endoparasitic, phytophagous nematodes (Esser, 1963).

Esser (1963) observed that the dorylaim predators rarely attacked or succeeded in devouring *Helicotylenchus* spp., and suggested some sort of chemical resistance in species of this genus. The present study supports these observations since wounded *Helicotylenchus indicus* were incompletely consumed more than any other prey species. Bilgrami and Jairajpuri (1988) also suggested the possibility of unfavourable secretions in *Helicoty-*

lenchus indicus which elicited meager responses of *M. fortidens* and *M. longicaudatus* besides *X. americanum* and *Longidorus* sp. The number of *Helicotylenchus indicus, X. americanum* and *Longidorus* sp., left unconsumed by the predators also suggests the presence of unfavourable/repellent substance(s) in the body of these species of prey. The texture of the cuticle of the dorylaims, *X. americanum, Longidorus* sp., may conform resistance to wounding. However, the strike rate against this group was also generally lower suggesting other defensive mechanisms may operate. It may be inferred from the present observations that *Hoplolaimus indicus, Trichodorus* sp., and *H. mangiferae* acquire physical resistance in the form of thick cuticle and annulations respectively; *Rhabditis* sp. behavioural resistance in the form of active body movements and vigorous escape response; *Helicotylenchus indicus* chemical resistance in the form of toxic/unfavourable secretions; and *X. americanum* and *Longidorus* sp., resisting predation partly by physical and chemical means.

Ectoparasitic nematodes living in close proximities to predacious nematodes may have developed more anti-predation devices. These mechanisms as mentioned above may be more effective against dorylaim, nygolaim actinolaim and diplogasterid predators since most of these predators possess piercing type of feeding apparatus and feed by puncturing the cuticle of prey. However, mononchs overcome the resistance of prey of different kinds to a larger extent as these do not puncture the cuticle of prey but engulf them whole. The ectoparasitic nematodes are therefore more vulnerable to predation by mononchs. This is evident as many species of mononchs have been found containing species of *Hoplolaimus, Helicotylenchus, Xiphinema, Hemicriconemoides, Rhabditis* sp., etc., besides other tylenchs, dorylaims, rhabditis and mononchs entire in their intestine (Bilgrami, Ahmad & Jairajpuri, 1986). Mohandas and Prabhoo (1980) also found intact *Tylenchorhynchus nudus* and *Xiphinema elongatum* in the intestine of *Iotonchus kherai* and *I. monohystera.*

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