Resistance and susceptibility of prey nematodes to predation and strike rate of the predators, Mononchus aquaticus, Dorylaimus stagnalis and Aquatides thornei

Anwar L. BILGRAMI

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

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Summary — The strike rate of the predators, Mononchus aquaticus, Dorylaimus stagnalis and Aquatides thornei and the degree of resistance and susceptibility of Acrobeloides sp. Cephalobus sp. Rhabditis sp., Panagrellus redivivus, Tylenchorhynchus mashhoodi, Hoplolaimus indicus, Helicotylenchus indicus, Scutellonema sp., Hemicycliophora sp., Hemicriconemoides mangiferae, Hirschmanniella oryzae, Longidorus sp., Paralongidorus citri, Paratrichodorus sp., Xiphinema americanum and the second stage juveniles of Meloidogyne incognita, Heterodera mothi and Anguina tritici to predation was measured and quantified using methods of Bilgrami and Jairajpuri (1989a). M. aquaticus was the most successful predator with maximum strike rate (SR = upto 100 %) on various species of nematodes. All saprophagous nematodes were highly susceptible to predation (PS > 90 %) except Rhabditis sp. which showed some degree of behavioural resistance in the form of active body undulations. Helicotylenchus indicus resisted predation by chemical means, i.e. toxic/unfavourable secretions. X. americanum, P. citri, Longidorus sp., and Paratrichodorus sp. are provided with physical characteristics (cf. cuticle) which provided partial resistance against predation. Hoplolaimus indicus, Scutellonema sp., Hemicycliophora sp. and H. mangiferae were totally resistant to predation by D. stagnalis and A. thornei; their individuals were neither injured nor killed by the two predators.

Résumé — Résistance et sensibilité à la prédation de nématodes-proies; taux d'agressivité des prédateurs Mononchus aquaticus, Dorylaimus stagnalis et Aquatides thornei — La méthode de Bilgrami et Jairajpuri (1989a) a permis de mesurer et de quantifier le taux d'agressivité des prédateurs Mononchus aquaticus, Dorylaimus stagnalis et Aquatides thornei ainsi que le degré de résistance ou de sensibilité des nématodes Acrobeloides spp., Cephalobus spp., Rhabditis spp., Panagrellus redivivus, Tylenchorhynchus mashhoodi, Hoplolaimus indicus, Helicotylenchus indicus, Scutellonema sp., Hemicycliophora sp., Hemicriconemoides mangiferae, Hirschmanniella oryzae, Longidorus sp., Paralongidorus citri, Paratrichodorus sp., Xiphinema americanum et des juvéniles de deuxième stade de Meloidogyne incognita, Heterodera mothi et Anguina tritici. M. aquaticus s'est montré le prédateur le plus performant avec un taux d'agressivité (SR) maximum (jusqu'à 100 %) envers différentes espèces de nématodes. Tous les nématodes saprophages sont très sensibles à la prédation (PS > 90 %) sauf Rhabditis sp. qui a un comportement de résistance grâce à des ondulations rapides du corps. Helicotylenchus indicus résiste à la prédation au moyen de substances chimiques (substances toxiques ou non favorables). X. americanum, P. citri, Longidorus sp., et Paratrichodorus sp. ont des caractéristiques physiques liées à la cuticule qui leur confèrent une résistance partielle contre la prédation. Hoplolaimus indicus, Scutellonema sp., Hemicycliophora sp. et H. mangiferae sont totalement résistants à la prédation par D. stagnalis et A. thornei; leurs individus ne sont en effet jamais blessés ou tués par ces deux prédateurs.

Key-words: Mononchus, Dorylaimus, Aquatides, prey nematodes, resistance, predation.

The predatory nematodes possess different mechanisms to overpower their prey and to feed upon them. Similarly, the prey nematodes also have characteristics, hereditory or acquired, to defend themselves from predation (Bilgrami, 1990 a, b; Jairajpuri & Bilgrami, 1990). The anti-predation adaptations are in the form of and behavioural physical. chemical istics (Esser, 1963, 1987; Esser & Sobers, 1964; Bilgrami & Jairajpuri, 1989a). Esser (1963) provided a list of resistant or susceptible prey nematodes to predation by different mononchs and dorylaims. Grootaert et al. (1977) measured susceptibility and resistance of tylenchid, areolaimid, enoplid and dorylaimid nematodes to predation while Small and Grootaert (1983) described their anti-predation adaptations. Very recently Bilgrami and Jairajpuri (1989a) have defined resistance and susceptibility of prey nematodes and strike rate of the predators and proposed methods to determine and quantify them using Mononchoides longicaudatus and M. fortidens as predators against a variety of free-living, ecto- and endo-parasitic nematodes. The present experiments were conducted to determine the degree of resistance and susceptibility of different trophic groups viz., saprophagous, ecto- and endoparasitic and predaceous nematodes to predation and the strike rate of the predators, Mononchus aquaticus, Dorylaimus stagnalis and Aquatides thornei.

Materials and methodes

The predaceous nematodes viz., Mononchus aquaticus (Mononchida), Dorylaimus stagnalis (Dorylaimina)

and Aquatides thornei (Nygolaimina) were cultured by the methods of Bilgrami and Jairajpuri (1988). The adult individuals of Acrobeloides sp., Cephalobus sp., Rhabditis sp., Panagrellus redivivus, Tylenchorhynchus mashhoodi, Hoplolaimus indicus, Helicotylenchus indicus, Scutellonema sp., Hemicycliophora sp., Hemicriconemoides mangiferae, Hirschmanniella oryzae, Paralongidorus citri, Longidorus sp., Paratrichodorus sp., Xiphinema americanum and the second stage juveniles of Meloidogyne incognita, Anguina tritici and Heterodera mothi were used as prey. The three predators were also used as prey against each other.

The ectoparasitic nematodes were isolated fresh from the soil by decantation and Baermann's funnel techniques for each experiment. The second stage juveniles of *M. incognita*, *H. mothi* and *A. tritici* were obtained from their populations maintained on tomato, moth grass and wheat galls respectively. The free living nematodes were obtained from the culture maintained in Petri-dishes containing 1 % water-agar supplemented with infant milk powder (Lactogen).

Fifty encounters were observed between predators and prev. The encounters (i.e., lip contact of predators with the prey at right angles) between predators and prey were observed in Petri-dishes containing 1 % water agar using a stereoscopic bionocular microscope. 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 predators in any manner. Only those observations were recorded where the predators behaved as normally as could be ensured. For each encounter a new predator and prey individuals were used (irrespective whether the predator failed or succeeded in attacking prey). To reduce the effect of satiation and prey habituation, 4-6 day starved predators were tested. The strike rate (SR) of the predators M. aquaticus, D. stagnalis and A. thornei and the degree of prey resistance (PR) and susceptibility (PS) to predation were determined using methods of Bilgrami and Jairajpuri (1989a). The percentage of predators which started feeding after wounding the prey and the prey which were left unconsumed by the predators were also determined (calculated respectively out of the total number of prey individuals

Results (Tables 1 and 2)

Resistance and susceptibility of prey to predation and strike rate of M. Aquaticus

Among saprophagous nematodes, encounters with P. redivivus, Cephalobus sp., and Acrobeloides sp., resulted in maximum strike rate (SR = 98 - 100 %) and prey wounding (AW = 98 - 100 %) while amongst endo parasitic nematodes M. aquaticus had maximum strike rate against A. tritici juveniles (SR = 98 %) with 98 % prey wounding. M. aquaticus was most successful

wounded and individuals upon which feeding actually

initiated). All species of predators were tested separately.

against T. mashhoodi and H. oryzae (SR = 92 - 94%) and wounded maximum individuals (AW = 93 - 94%) in comparison to other ecto-parasitic nematodes. M. aquaticus exhibited high degree of success upon their own individuals (SR = 88%) but not on other predators viz., D. stagnalis and A. thornei. Hoplolaimus indicus (PR = 87 %); Scutellonema sp. (PR = 91 %); D. stagnalis(PR = 83 %) and A. thornei (PR = 88 %) were most resistant prey species while T. mashhoodi (PS = 93 %), H. oryzae (PS = 94 %); A. tritici juv. (PS = 98 %); M. incognita juv. (PS = 100 %); H. mothi juv. (PS = 96 %); P. redivivus (PS = 98 %); Cephalobus sp. (PS = 98 %); Acrobeloides sp., (PS = 100 %) and Longidorus sp. (PS = 91 %) were highly susceptible species of prey nematodes to predation. Predators which started feeding upon prey after wounding was maximum (FW = 100 %) on P. redivivus, Cephalobus sp., Acrobeloides sp., Rhabditis sp., A. tritici, and M. incognita juveniles. Feeding after wounding (FW) H. oryzae, T. mashhoodi and H. oryzae was 91 % and 95 % respectively, while that on other prey nematodes ranged between 50-89 %. M. aquaticus though wounded, 80 % of Helicotylenchus indicus but fed upon 25 % of individuals leaving 60 % of them either unconsumed or partially eaten. 36 % individuals of H. mangiferae and 23 % of Scutellonema sp., were also left unconsumed by the predators. Other prey species were left unconsumed in lesser numbers (0-16 %). M. aquaticus took a minimum of 7-11 (9) min and 8-15 (10) min to consume completely an individual of M. incognita and Acrobeloides sp., respectively and maximum of 86-113 (96) min to finish D. stagnalis.

RESISTANCE AND SUSCEPTIBILITY OF PREY TO PREDATION AND STRIKE RATE OF D. STAGNALIS

Encounters with M. incognita, H. mothi and A. tritici juveniles yielded maximum success (SR = 82 %; 80 % and 82 %) and wounding (AW = 93 %, 80 % and 90 %) respectively. Among ectoparasitic nematodes D. stagnalis attacked T. mashhoodi with maximum success (SR = 84 %) and wounding (AW = 86 %). Encounters with saprophagous nematodes yielded maximum success with Cephalobus sp., (SR = 80 %) but more P. redivivus were wounded by the predators (AW = 95 %). With others it resulted into a moderate to high rate of wounding (AW = 5-90 %). D. stagnalis failed to wound any individuals of Hoplolaimus indicus, Scutellonema sp., H. mangiferae, Hemicycliophora sp., and D. stagnalis (PR = 100 %). P. redivivus, Cephalobus sp., A. tritici and M. incognita juveniles were highly susceptible to predation by D. stagnalis (PS = 90-95%). Acrobeloides sp., T. mashoodi sp., H. oryzae, H. mothi, X. americanum, Longidorus sp., Paratrichodorus sp., possessed low to moderate degree of resistance (PR = 10-24 %). Rhabditis sp., and Helicotylenchus indicus exhibited moderate to high degree of resistance (PR = 30-53 %) against predation. D. stagnalis initiated feeding upon

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Table 1. Strike rate of Mononchus aquaticus (MA); Dorylaimus stagnalis (DS); Aquatides thornei (AT) and resistance and susceptibility of prey to predation.

Prey	Predators	EA	SR (ⁱ⁾ _i)	Wounding			Feeding		Duration of
				AW (%)	PR (%)	PS ("e)	FW ()	prey left-un consumed ("")	feeding upon single prey (min)
APROPHAGOUS NEMATODES									
P. redivivus	MA	50	100	98	2	98	100	0	10-16 (13)
	DS	38	76	95	5	95	78	7	9-15 (14)
	AT	40	80	95	5	95	88	6	8-12 (10)
Cephalobus sp.	MA	50	100	98	2	98	100	0	13-19 (16)
	DS	40	80	90	10	90	67	8	14-22 (19)
	AT	42	84	93	7	93	82	3	12-16 (15)
Acrobeloides sp.	MA	49	98	100	0	100	100	0	8-16 (15)
	DS	35	70	89	11	89	71	9	10-17 (15)
	AT	36	72	94	6	94	82	4	10-22 (14)
Rhabditis sp.	MA	44	88	86	14	86	100	5	19-26 (23)
	DS	39	78	67	33	67	77	15	26-34 (30)
	AT	42	84	76	24	76	78	8	20-24 (22)
CTOPARASITIC NEMATODES									
T. mashhoodi	MA	46	92	93	7	93	95	4	14-26 (19)
	DS	42	84	86	14	86	77	7	22-38 (28)
	AT	44	88	89	11	89	69	7	18-32 (30)
H. oryzae	MA	47	94	94	6	94	91	10	22-34 (30)
	DS	37	74	86	14	86	26	12	31-47 (36)
	AT	39	78	90	10	90	86	3	30-49 (39)
Hoplolaimus indicus	MA	46	92	13	87	13	77	10	30-51 (41)
	DS	41	82	0	100	0	0	0	0
	AT	37	74	0	100	0	0	0	0
Helicotylenchus indicus	MA	45	90	89	11	89	25	40	35-42 (37)
	DS	40	80	47	53	47	31	33	39-56 (46)
	AT	42	84	52	48	52	36	88	30-52 (39)
Scutellonema sp.	MA	44	88	9	91	9	67	23	29-49 (39)
	DS	40	80	0	100	0	0	0	0
	AT	42	84	0	100	0	0	0	0
H. mangiferae	MA	39	78	41	59	41	50	36	24-29 (26)
	DS	32	64	0	100	0	0	0	0
	AT	34	68	0	100	0	0	0	0
Hemicycliophora sp.	MA	42	84	33	67	33	50	13	20-33 (28)
	DS	33	66	0	100	0	0	0	0
	AT	36	72	0	100	0	0	0	0
X. americanum	MA	43	86	84	16	84	72	3	28-43 (37)
	DS	34	68	76	24	76	69	7	42-63 (52)
	AT	32	64	91	19	91	83	13	38-69 (52)
Longidorus sp.	MA	43	86	91	9	91	79	12	41-56 (48)
	DS	34	68	76	24	76	69	22	50-66 (57)
	AT	36	72	33	33	67	75	22	44-84 (68)
P. citri	MA	43	86	84	16	84	89	16	46-59 (51)
	DS	34	68	85	15	85	52	26	58-72 (66)
	AT	33	66	76	24	76	84	29	61-94 (72)
Paratrichodorus	MA	45	90	91	9	91	88	9	25-34 (30)
	DS	38	76	42	58	42	81	13	34-46 (42)
	AT	36	72	44	56	44	81	13	31-49 (41)

All figures are in nearest whole numbers; Figures in paranthesis indicate mean feeding time.

EA = Encounters resulted into attack; AW = Attacks resulted into prey wounding; PS = Prey susceptibility to predation; SR = Strike rate of predators; PR = Prey resistance to predation; FW = Feeding after wounding prey.

Table 2. Strike rate of Mononchus aquaticus (MA); Dorylaimus stagnalis (DS); Aquatides thornei (AT) and resistance and susceptibility of prey to predation.

Prey	Predators	EA	SR (%)	Wounding			Feeding		Duration of
				AW (%)	PR ("o)	PS (%)	FW (%)	prey left-un consumed (%)	feeding upon single prey (min)
ENDO-PARASITIC NEMATODES									
	MA	49	98	98	2	98	100	13	8-14 (11)
A. tritici	DS	40	90	90	10	90	83	10	12-28 (20)
	AT	42	93	78	7	93	85	6	10-26 (18)
	MA	48	96	100	0	100	100	2	7-14 (9)
M. incognita	DS	41	82	93	7	93	74	7	16-32 (24)
	AT	41	82	95	5	95	77	3	12-30 (21)
	MA	48	96	85	4	96	96	6	8-15 (10)
H. nothi	DS	40	80	80	20	80	90	18	15-30 (21)
	AT	42	84	86	14	86	33	6	12-24 (18)
REDATORY NEMATODES									
	MA	30	60	17	83	17	60	8	86-113 (96)
D. stagnalis	DS	5	10	0	100	0	0	0	0 '
	AT	14	28	0	100	0	0	0	0
	MA	32	64	12	8	12	71	0	59-78 (64)
A. thornei	DS	7	14	0	100	0	0	0	
	AT	8	16	0	100	0	0	0	0
	MA	44	88	68	32	68	67	0	47-62 (52)
M. aquaticus	DS	19	38	5	95	5	100	0	34 (34)
	AT	18	36	0	100	0	0	0	0

All figures are in nearest whole numbers; Figures in parentheseis indicate mean feeding time.

EA = Encounters resulted into attack; AW = Attacks resulted into prey wounding; PS = Prey susceptibility to predation; SR = Strike rate of predators; PR = Prey resistance to predation; FW = Feeding after wounding prey.

31% of individuals belonging to Helicotylenchus indicus but 33% of them were left unconsumed. Maximum feeding occurred on H. mothi juveniles (FW = 90%) and Trichodorus sp. (FW = 81%). D. stagnalis took a minimum time of 9-15 (14) min to consume completely an individual of P. redivivus and maximum of 58-72 (60) min to finish P. citri.

Resistance and susceptibility of prey to predation and strike rate of A. Thornei

A. thornei attacked all species of prey nematodes with highest strike rate (SR = 84 %) on Rhabditis sp., among saprophagous nematodes; 82-84 % on the second stage juveniles of endo-parasitic nematodes, M. incognita, H. mothi and A. tritici and 88 % on ectoparasitic nematodes, T. mashhoodi. A. thornei was least successfull on D. stagnalis, M. aquaticus and upon its own individuals (SR = 16-36 %). Hoplolaimus indicus, Scutellonema sp. Hemicycliophora sp., D. stagnalis, M. aquaticus and A. thornei were totally resistant to predation by A. thornei (PR = 100 %. P. redivivus, Cephalobus sp.,

Acrobeloides sp., H. oryzae and the second stages of M. incognita, H. mothi and A. tritici were most vulnerable species of prey (PS = 86-95 %). Rhabditis sp., T. mashhoodi, Helicotylenchus indicus, X. americanum, P. citri, Longidorus sp., and Paratrichodorus sp., possessed low to moderate degree of resistance (PR = 10-50 %). Maximum feeding occurred on Cephalobus sp. (FW = 82 %), A. tritici (FW = 77 %) and H. oryzae (FW = 86 %) among different trophic groups of prey. A. thornei initiated feeding only upon 36 % individuals of Helicotylenchus indicus but left maximum of them unconsumed (88 %). The number of individuals of P. redivivus, Cephalobus sp., Acrobeloides sp., Rhabditis sp., T. mashhoodi, H. oryzae, H. mothi and M. incognita juveniles left unconsumed were significantly low (3-8 %, p < 0.05). However, comparatively, greater number of individuals of X. americanum (13%); Longidorus sp. (22 %), P. citri and Paratrichodorus sp. (13 %), were left partially consumed. A. thornei required a maximum of 61-94 (72) min to consume an individual of Paralongidorus citri and minimum of 8-12 (10) min to finish P. redivivus.

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Discussion

Wounding is an important factor in predation (Bilgrami & Jairajpuri, 1989a). Small and Grootaert (1983) and Esser (1987) also suggested that resistance of a prey is lost if wounded or in a weakened condition. A wound may also 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. Thus, it is the wounding which determines the degree of resistance and susceptibility of a prey and ability of predators more precisely and hence, was considered as the primary determinant.

The prey nematodes can resist predation by physical, chemical and behavioural characteristics (Esser, 1963, 1987; Esser & Sobers, 1964; Bilgrami & Jairajpuri, 1989a) such as thick cuticle (Esser, 1963; Small & Grootaert, 1983), annulations in criconematids (Esser, 1963; Bilgrami & Jairajpuri, 1989a); gelatinous matrix (Small & Grootaert, 1983); speed (Esser, 1963; Bilgrami & Jairaipuri, 1989a); vigorous escape response (Grootaert et al., 1977; Small & Grootaert, 1983; Bilgrami & Jairajpuri, 1989a) and toxic/unfavourable secretions (Esser, 1963; Bilgrami & Jairajpuri, 1989a). The environmental soil factors e.g., temperature, pH, moisture, soil type, chemical composition of soil, etc., also play a significant role in governing activities of predators as is evident from experiments on temperature (Wallace, 1969; Bilgrami et al., 1983); crowding (Azmi & Jairajpuri, 1979), chemicals (Bilgrami & Jairajpuri, 1985a), pH (Bilgrami & Jairajpuri, 1985a) and soil types (Small, 1979).

During present study the high susceptibility of P. redivivus sp., Cephalobus sp., M. incognita, A. tritici and H. mothi juveniles to predation by M. aquaticus, D. stagnalis and A. thornei may be attributed to their small body size, slow rate of movement (Bilgrami et al., 1983) and lack of anti-predation devices (Small & Grootaert, 1983). The ecto-parasitic nematodes seem to be more vulnerable to predation specially by mononchs. This is evident as many species of mononchs have been found containing resistant species of nematodes viz., Hoplolaimus, Helicotylenchus, Scutellonema, Hemicriconemoides, Hemicycliophora, Rhabditis, Xiphinema, etc., entire in their intestine besides many other tylenchs, dorylaims, mononchs and rhabditids (Bilgrami et al., 1986). No predation on Hoplolaimus indicus, Scutellonema, H. mangiferae and Hemicycliophora sp., by D. stagnalis and A. thornei suggests resistance due to thick cuticle and annulations (physical resistance) (Bilgrami & Jairajpuri, 1989a). Moderate to high degree of resistance (PR = 24-58 %) in Paratrichodorus sp., Longidorus sp., P. citri and X. americanum to predation by D. stagnalis and A. thornei appeared to be of physical nature. D. stagnalis also possessed physical resistance in the form of thick and tough cuticle.

Esser (1963) suggested chemical resistance in the species of Helicotylenchus as he observed dorylaim predators rarely attacking or succeeding in devouring the individuals of Helicotylenchus spp. The meagre responses of Mononchoides longicaudatus and M. fortidens towards Helicotylenchus indicus - live or excised — (Bilgrami & Jairajpuri, 1988), their inhibited feeding and leaving greater number of wounded prey unconsumed (Bilgrami & Jairajpuri, 1989a, 1990) support chemical resistance in Helicotylenchus indicus. The same has been observed during present investigations except in M. aquaticus which wounded and killed a large population of Helicotylenchus indicus and fed equally upon them, leaving least number of prey unconsumed. This disparity is possible specially with mononchs as 1) they are capable to overcome resistance of varying types (Bilgrami & Jairaipuri, 1989a); 2) their predation/feeding is aleatory (Bilgrami et al., 1986) depending exclusively on chance encounters (governed mostly by mechanoreceptors) and 3) no evidence of chemical perception (prey secretions) is available in mononchs (Bilgrami et al., 1984). In contrast, the dorylaim (Esser, 1963; Shafqat et al., 1987), nygolaim (Bilgrami et al., 1985) and diplogasterid predators (Bilgrami & Jairajpuri, 1988; able to perceive prey secretions, attracted towards them and aggregated around a previously injured prey at feeding sites (Bilgrami & Jairajpuri, 1989b).

Rhabditis oxycerca, Pelodera and Plectus sp., possess characteristics such as active body undulations and vigorous escape response which provide resistance against predation (Small & Grootaert, 1983). Rhabditis sp., seems to rely primarily on active body undulations and vigorous escape response to resist predation by M. aquaticus, D. stagnalis and A. thornei as is evident by the combination of high strike rate of the three species of predators against Rhabditis sp., and comparatively lower rate of wounding and higher rate of feeding upon wounded prey individuals. The abilities of predators themselves govern their efficiency as predators and also the degree to overcome prey resistance as some predators possess strong predatory potentials. This is evident from the present observations on M. aquaticus which showed maximum strike rate upon all the prev nematodes and almost all prey nematodes were most susceptible to M. aquaticus in comparison to D. stagnalis and A. thornei.

M. aquaticus avoided predation by other predators viz., D. stagnalis and A. thornei mainly with its active body undulations (behavioural resistance). However, their high degree of susceptibility to predation by their own members conforms cannibalistic tendency in mononchs as has been reported earlier (Azmi & Jairajpuri, 1979; Bilgrami & Jairajpuri, 1985b; Bilgrami et al., 1986). The phenomenon of cannibalism is not evident either in D. stagnalis or A. thornei (Shafqat et al., 1987; Bilgrami et al., 1985).

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