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CHEMOSENSORY RESPONSES OF PREDATORY NEMATODES TOWARDS KAIROMONES EMITTED BY PREY NEMATODES BELONGING TO DIFFERENT TROPHIC GROUPS

by
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Summary. Observations were made on the attraction and migration of *Mesodorylaimus bastiani* and *Aquatides thornei* towards kairomones/attractants emitted by prey nematodes belonging to different trophic categories viz., saprophagous, predators and epidermal, endodermal, migratory semi-endodermal and cortical feeders. Both species of predators responded positively and significantly to prey kairomones but showed variations in their attraction and preferential behaviour. Predators responded maximally towards excised prey individuals. As a prey trophic group the epidermal feeders were most attractive to predators whereas migratory semi-endodermal feeders were the least. The differential responses of predators towards different species of prey are attributed to differences in the inert behaviour of predators, their preference for a particular species of prey and chemical composition, concentration, quality and quantity of prey attractants and formation of minimum perceptible attraction gradient by prey attractants and minimum response threshold of predators. Various factors such as prey density, period of prey incubation and starvation of predators, temperature, agar concentration, agar thickness and distance of predators from the source of attraction (prey) governed chemosensory responses of predators. Both species of nematodes responded maximally towards prey kairomones when tested as ten day starved predators in agar plates containing 2 mm thick layer of 1% water agar with 200 prey individuals previously incubated for 12-16 h at 30 °C. Prey kairomones were most attractive when *M. bastiani* and *A. thornei* were tested at a distance of 2 to 3 cm.

Observations made by Yeates (1969), Bilgrami *et al.* (1985b) and Shafqat *et al.* (1987) suggested that predatory nematodes make chemosensory responses to prey secretions. A detailed study on the chemonsensory responses of predatory nematodes revealed attraction and aggregation of diplogasterid predators, *Mononchoides fortidens* and *M. longicaudatus* due to attractants emitted by the prey individuals (Bilgrami and Jairajpuri, 1988; 1989b, 1989c). In the case of predatory nematodes characteristics like prey searching and chemoattraction are important attributes which are directly related to their predatory potential and field efficacy. Such characteristics can be exploited to incorporate biotechnological techniques to focus on the modification of behaviour of predatory nematodes as a means of nematode pest management.

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Prey kairomones/attractants are chemicals which are secreted into the environment to bring together the predator and prey individuals and induce favourable behavioural and physiological response in receiver organisms (Green, 1980, Heuttel, 1986).

In view of the sparse knowledge on chemosensory behaviour of predatory nematodes, the following experiments were made to investigate attraction and preferential behaviour of two species of predatory nematodes *viz.*, *Aquatides thornei* (Schneider) Ahmad *et* Jairajpuri (a nygolaim) and *Mesodorylaimus bastiani* (Butschli) Andrassy (a dorylaim) in response to kairomones/attractants emitted by prey nematodes belonging to different trophic groups.

Materials and methods

In vitro cultures of *M. bastiani* and *A. thornei* were maintained on *Rhabditis* sp., in Petri dishes containing 1% agar. To permit growth of bacterial populations, to serve as food for the prey nematodes, 5 mg infant milk powder (Lactogen) was spread over the surface of the agar.

To test chemosensory responses of *M. bastiani* and *A. thornei* towards attractants/kairomones emitted by prey nematodes belonging to different trophic groups (Table I), experiments were made in 5.5 cm diam. Petri dishes, divided into inner, middle and outer circles by drawing two concentric circles 0.5 and 2.5 cm in diam. on the bottom surface. Normal experimental temperature was 28±2 °C. A plastic straw pipe 5 mm high, 5 mm in diam. with one end sealed with a piece of 400 mesh sieve (to restrict prey nematodes within the tube) was placed vertically in the inner circle to leave the sealed end in contact with the bottom of the dish. Autoclaved 1% water agar was poured into the Petri dishes and straw pipe to make a 2 mm thick agar layer. Prey nematodes (Table I) were extracted fresh from the soil and surface sterilized with 0.01% mercuric chloride. Twenty five live or excised (cut in two pieces) prey nematodes were incubated in the straw pipe for 16 h. Five adult predators were then released at the periphery of the middle circle. The distribution of predators was recorded after 6 h and scores were obtained by summing up the product of the number of nematodes in each zone with their corresponding weighted factors. The weighted factors were obtained by dividing the area of the outer zone by that of each of the three zones (Bilgrami and Jairajpuri, 1988). Each experiment

TABLE I - *List of nematodes used as prey.*

Trophic group	Genera and species
Saprophagous	*Rhabditis sp.*, *Acrobeloides sp.*, *Cephalobus sp.*
Endodermal feeders	Second stage juveniles of *Meloidogyne incognita* (Kofoid *et* White) Chitw., *Anguina tritici* (Steinbuch) Filipjev, *Heterodera mothi* Khan *et* Hussain
Migratory semi-endodermal	*Hirschmanniella oryzae* (van Breda de Haan) Luc *et* Goodey, *Hoplolaimus indicus* Sher, *Helicotylenchus indicus* Siddiqi
Epidermal feeders	*Tylenchorhynchus mashhoodi* Siddiqi *et* Basir, *Basiria graminiphola* Siddiqi, *Aphlenchoides sp.*
Cortical feeders	*Hemicriconemoides mangiferae* Siddiqi, *Hemicycliophora dhirendri* Hussain *et* Khan
Predators	*Mesodorylaimus bastiani* (Butschli) Andrassy, *Aquatides thornei* (Schneider) Ahmad *et* Jairajpuri, *Discolaimus major* Thorne

was replicated 40 times. The scores were then converted into log scores. The log scores of all 40 replicates were summed up and the mean was calculated; referred to here as the mean log score. Therefore, the mean log score is the scale at which the attraction responses of predators were measured and compared. Both species of predators were tested separately with each species of prey. Two sets of experiments were performed. In the first, excised (cut in two pieces) prey nematodes were used, while in the second set non-excised (intact and live) individuals were used. For the definition of prey trophic groups viz., saprophagous, epidermal, cortical, endodermal, migratory semi endodermal, and predaceous nematodes the system of Bilgrami (1993, 1995) and Yeates *et al.* (1993) was followed. The responses of *M. bastiani* and *A. thornei* were tested separately towards excised and non-excised prey nematodes (Table I). The above conditions remained the same for all experiments unless otherwise mentioned.

The Effect of prey numbers on the attraction responses of *M. bastiani* and *A. thornei* was observed by incubating 25, 50, 75, 100, 125, 150, 175, 200, 225 and 250 individuals of *Hirschmanniella oryzae* or *Meloidogyne incognita* in the straw pipes in separate sets of Petri dishes.

Prey nematodes belonging to *H. oryzae* or *M. incognita* were incubated at 5, 10, 15, 20, 25, 30, 35 and 40 °C to determine the effect of temperature on the degree of attraction of *M. bastiani* and *A. thornei* towards kairomones emitted by prey individuals. Each species of predator was tested separately, using one species of prey at a time.

Individuals belonging to *H. oryzae* or *M. incognita* were incubated separately by releasing them in the straw pipe of separate Petri dishes for 4, 8, 12, 16, 20, and 24 h to observe the effects of the period of incubation of prey kairomones on the attraction of *M. bastiani* and *A. thornei.*

M. bastiani and *A. thornei* were starved for 0 (fresh), 2, 4, 6, 8 and 10 days by releasing them in cavity blocks containing water (without prey nematodes). Predators were transferred to fresh water each day. Day 0 refers to fresh predators (well fed). Each group of starving predators was tested separately towards previously incubated prey individuals belonging to *H. oryzae* or *M. incognita.*

The effect of different concentrations of agar on the degree of attraction of *M. bastiani* or *A. thornei* was tested in Petri dishes containing agar layers of 1, 2, 3, 4, 5 and 6% concentrations.

M. bastiani and *A. thornei* were released in Petri dishes containing 2, 4, 6, 8 and 10 mm thick agar layers incubated previously with the required number of prey individuals to determine their influence on the attraction responses of predators.

The effect of distance of inoculation of predators from the prey on their attraction was tested in 7 cm diam. Petri dishes. The dishes were marked on the bottom with straight lines in seven zones and numbered serially as 1, 2, 3...7 (Bilgrami *et al.*, 1985a). A plastic straw pipe, one end sealed with a piece of filter paper, was placed vertically in zone 1. The sealed end remained inside the agar. Twenty five prey nematodes were released in the straw pipe and incubated for 16 h. Twenty five predators were then released at different points in zone 2. The number of predators present in each zone was recorded after 6 h. Similarly, in other sets of Petri dishes the responses of the predators were tested by releasing them in zones 3, 4, 5, 6 and 7.

Results and discussion

M. bastiani and *A. thornei* exhibited attraction in response to kairomones/attractants dispersed by prey individuals belonging to different trophic groups. Excised individuals of all prey species were more attractive to predators than their live or intact members.

The excised and non-excised individuals of *Rhabditis* sp. belonging to saprophagous nematodes attracted *M. bastiani* the most, while *Acrobeloides* sp. the least ($p<0.05$) (Table II A).

TABLE II - *Chemosensory responses of* Mesodorylaimus bastiani *and* Aquatides thornei *towards excised and non-excised individuals of prey belonging to different trophic groups (n=40).*

Prey trophic Category	*M. bastiani*				*A. thornei*			
	Excised M±SD Range	CV (%)	Non-excised M±SD Range	CV (%)	Excised M±SD Range	CV (%)	Non-excised M±SD Range	CV (%)
A-Saprophagous nematodes								
Rhabditis sp.	2.21±0.13 (2.00-2.30)	6	2.08±0.11 (2.00-2.28)	5	2.30±0.04 (2.28-2.45)	2	2.19±0.16 (2.00-2.45)	7
Cephalobus sp.	2.12±0.14 (2.00-2.28)	6	1.95±0.18 (1.30-2.04)	9	2.19±0.20 (1.99-2.45)	9	2.10±0.13 (2.01-2.29)	6
Acrobeloides sp.	1.91±0.25 (1.30-2.04)	8	1.81±0.31 (1.30-2.00)	18	1.95±0.18 (1.30-2.02)	9	1.90±0.24 (1.30-2.00)	13
B. Epidermal feeders								
T. mashhoodi	2.17±0.16 (1.99-2.45)	7	2.06±0.11 (1.30-2.30)	5	2.27±0.21 (2.04-2.46)	9	2.21±0.19 (2.01-2.45)	8
B. graminifola	2.30±0.13 (2.02-2.46)	6	2.19±0.15 (1.30-2.45)	7	2.22±0.17 (1.99-2.45)	8	2.07±0.13 (1.99-2.30)	6
Aphelenchoides sp.	2.24±0.14 (2.01-2.46)	6	2.05±0.35 (1.30-2.30)	17	2.25±0.20 (2.04-2.45)	9	2.18±0.14 (2.02-2.30)	6
C. Migratory semi endodermal feeders								
H. oryzae	2.30±0.13 (2.02-2.46)	6	2.13±0.13 (2.00-2.30)	6	2.30±0.16 (2.04-2.45)	7	2.21±0.19 (2.00-2.45)	8
Hel. indicus	1.48±0.34 (1.23-2.04)	23	1.67±0.35 (1.30-2.00)	21	1.74±0.40 (1.30-2.04)	23	1.94±0.37 (1.30-2.30)	19
Hop. indicus	2.16±0.18 (2.00-2.46)	8	2.01±0.22 (1.30-2.30)	11	2.21±0.18 (2.00-2.45)	8	2.14±0.15 (2.00-2.30)	7
D. Cortical feeders								
H. mangiferae	2.02±0.22 (1.30-2.28)	11	1.96±0.18 (1.30-2.04)	9	2.08±0.12 (2.00-2.30)	6	2.00±0.02 (1.99-2.04)	1
H. dhirendri	2.01±0.23 (1.30-2.29)	11	1.90±0.24 (1.30-2.02)	13	2.10±0.15 (1.99-2.29)	7	2.05±0.13 (1.99-2.29)	6
E. Endodermal feeders								
M. incognita	2.19±0.15 (1.30-2.46)	7	2.04±0.09 (1.99-2.29)	4	2.21±0.2 (1.99-2.45)	9	2.11±0.16 (1.99-2.30)	7
A. tritici	2.23±0.11 (1.99-2.30)	5	2.15±0.14 (1.99-2.99)	6	2.18±0.14 (2.02-2.45)	6	2.13±0.15 (2.00-2.30)	7
H. mothi	2.05±0.35 (1.30-2.30)	7	1.90±0.32 (1.30-2.28)	17	2.05±0.12 (1.99-2.28)	6	1.94±0.37 (1.30-2.28)	19
F. Predators								
M. bastiani	2.09±0.12 (2.00-2.29)	6	1.96±0.18 (1.30-2.29)	9	2.01±0.02 (1.99-2.04)	1	1.88±0.32 (1.30-2.04)	17
A. thornei	2.13±0.13 (2.00-2.30)	6	2.02±0.24 (1.30-2.46)	12	2.09±0.20 (1.99-2.45)	9	1.86±0.31 (1.30-2.04)	17
D. major	2.20±0.13 (2.00-2.30)	6	2.08±0.1 (2.00-2.30)	5	2.13±0.15 (2.00-2.30)	7	2.02±0.44 (1.30-2.30)	22

MLS±SD=Mean log score with standard deviation; figures in parenthesis show the range; CV=Coefficient of variations; CV values are nearest to whole numbers. The figures presented in the table are Mean Log Scores derived from the distribution of nematodes in the Petri dish and are presumed as the chemosensory response of predators.

A. thornei responded identically to excised and non-excised individuals of *Rhabditis* sp. ($p<0.05$).

Excised individuals of *Aphelenchoides* sp., belonging to epidermal feeders elicited maximum response from *M. bastiani* and *A. thornei* ($p<0.05$). Similarly, non-excised nematodes elicited maximum degree of attraction by these predators ($p<0.05$) (Table II B).

When migratory semi-endodermal feeders were tested as prey, maximum attraction of *M. bastiani* and *A. thornei* was recorded towards excised individuals of *H. oryzae* ($p<0.05$) (Table II C). Non-excised *Helicotylenchus indicus* were attractive but predators showed repulsive behaviour in their presence.

M. bastiani responded identically towards excised and non-excised individuals of *Hemicriconemoides mangiferae* and *Hemicycliophora dhirendri* ($p<0.05$) (Table II D). *A. thornei* behaved differently towards excised and non-excised individuals of cortical feeders preferring *H. mangiferae* ($p<0.05$).

Among endodermal feeders, *M. bastiani* preferred *Heterodera mothi* whereas, *A. thornei* showed preference for the excised individuals of *Anguina tritici* ($p<0.05$). *M. incognita* was least attractive to the predators (Table II E).

A. thornei and *M. bastiani* responded maximally towards their own excised and non-excised members ($p<0.05$) (Table II F). *M. bastiani* when used as prey was least attractive to *A. thornei.*

These studies with *M. bastiani* and *A. thornei* showed their positive responses towards kairomones emitted by prey nematodes belonging to different trophic groups. The migration of *M. bastiani* and *A. thornei* towards prey attractants may therefore be attributed to their chemosensory mechanisms (chemotactic response). In the present observations *A. thornei* was more responsive, an exception being *H. indicus* and *Acrobeloides* sp. This differential response may be attributed to the inert behaviour of predators, their preference for the prey, chemical composition, concentration, quality and quantity of prey secretions and minimum perceptible attraction gradient of prey attractants besides minimum response threshold of predators (Bilgrami, 1992; 1993; 1995). Such characteristics show interspecific and intraspecific variations (Doncaster and Seymour, 1973; Jairajpuri and Bilgrami, 1990). The chemical composition of prey individuals may be determined by a number of physiochemical factors, especially the ageing and starvation of prey individuals (Cooper and Van Gundy, 1970; Reversat, 1981a; 1981b) and food and feeding habits of predators and prey (Bilgrami *et al.*, 1986; Yeates and Wardle 1996).

Differential responses of *M. bastiani* and *A. thornei*, both when used as predators or as prey animals, may have been due to specific differences in their minimum response threshold in their former role, and in minimum perceptible attraction gradient in their latter role. In the present observations *H. indicus* appeared to possess higher concentrations of allomones/repellents. Meager responses shown by predators towards *H. indicus* are in sharp contrast to what these predators showed towards excised prey individuals belonging to other genera. Such a response of predators conforms with the low rate of predation by many species of predators, including *A. thornei* on *H. indicus* (Bilgrami *et al.*, 1985b; Bilgrami and Jairajpuri, 1989a). Maximum attraction of *M. bastiani* and *A. thornei* towards *Rhabditis sp.*, *H. oryzae*, *H. mothi*, *H. mangiferae* and *M. bastiani* suggest that they posses kairomones/attractants in favourably higher concentrations. *Acrobeloides sp.*, *Tylenchorhynchus mashhoodi*, *A. tritici* and *H. dhirendri* were moderately attractive species of their respective prey trophic groups.

Prey density, incubation period of prey, starvation of predators, temperature, agar concentration, agar thickness and distance of predators governed the degree of attraction of *M. bastiani* and *A. thornei* towards attractants/kairomones emitted by the prey nematodes. Mean Log Score for the two species of predators during control experiments ranged between 1.21 to 1.34 for the above mentioned factors except agar concentration where it was 1.12-1.28.

M. bastiani was attracted maximally towards attractants emitted by *H. oryzae* and *M. incognita* at 30 °C ($p<0.05$) (Fig. 1 A). Temperatures higher than 30 °C inhibited attraction of predators towards prey. *A. thornei* exhibited similar responses at different temperatures towards *H. oryzae* or *M. incognita* ($r=0.79$ and 0.75; PEr=0.006-0.007 respectively, $p<0.05$) (Fig. 1 B). Decreased attraction of *M. bastiani* and *A. thornei* at temperatures less than 25 °C and more than 35 °C may be attributed firstly to their inhibited activity (Wallace, 1969; Azmi and Jairajpuri, 1977; Bilgrami *et al.*, 1983) and secondly to the slow rate of dispersion of prey kairomones due to unfavourable temperatures. Lower and higher temperatures appeared to have influenced the rate of dispersion of prey kairomones and formation of minimum perceptible attraction gradient and altered the optimum minimum response threshold level in predators.

Short (4 h) and long duration (24 h) of incubation of prey attractants yielded the lowest degree of attraction of *M. bastiani* and *A. thornei* (Fig. 1 C and D). The degree of attraction increased when prey nematodes were incubated for 8 to 20 h ($p<0.05$). The 12 to 16 h prey incubation yielded a maximum response from *M. bastiani* and *A. thornei.* The disparity may be attributed to the formation of a minimum perceptible attraction gradient by prey kairomones as well as the minimum response threshold of the predators. Such characteristics showed inter and intraspecific variations. In some, the intensity may be high while in others it may be low. Individuals with a low perception threshold level could perceive attractants early from long distances while those having high threshold levels could take a longer time to perceive stimuli even from shorter distances (Bilgrami and Jairajpuri, 1988).

M. bastiani and *A. thornei* exhibited a high degree of correlation between the attraction and number of prey individuals incubated ($r=0.76$-0.95; PEr=0.007; $p<0.05$) (Fig. 1 E and F). Maximum attraction was recorded towards a population of 200 prey individuals ($p<0.05$) and minimum when 25 individuals of *H. oryzae* or *M. incognita* were used as prey. Thus, when prey nematodes were plentiful, kairomones/attractants had a greater positive impact on attraction responses of *M. bastiani* and *A. thornei* than when prey individuals were scarce. This may be due to the lower or higher mean concentration of attractants at low or high prey densities, respectively, occurring due to decreased or increased biomass, respectively. Attractants with the latter possibility may be dispersed in the wider area and develop minimum perceptible attraction gradients quickly, thus remaining effective for a long duration and hence eliciting greater response of predators.

Increased period of starvation of predators stimulated a more active search for prey ($r=0.76$-0.99; PEr=0.0003-0.007; $p<0.05$) (Fig. 2 A and B) as they could sense weaker stimuli due to decrease in minimum response threshold level (Doncaster and Seymour, 1973; Bilgrami and Jairajpuri, 1985a). A phenomenon which could be substantiated with increased predation by starving dorylaims (Khan *et al.*, 1996) and nygolaims (Bilgrami *et al.*, 1985b). Degree of attraction increased significantly from 0 day (fresh) to 10th day of starvation of predators ($P<0.05$).

Degree of attraction of *M. bastiani* and *A. thornei* decreased with the increase in agar concentration ($r = -0.95$ to -0.98; PEr=0.0006-0.0016; $p<0.05$) (Fig. 2 C and D). Predators were attracted maximally towards prey at 1-2% agar concentrations. Higher concentrations inhibited attraction.

Attraction decreased with the increase in the thickness of agar ($r = -0.96$ to -0.99; PEr=0.0003-0.001; $p<0.05$) (Fig. 2 E and F). An agar layer of 2 mm thickness favoured attraction of the two species of predators most and 12 mm the least ($p<0.05$). *H. oryzae* was more attractive to predators than *M. incognita.* Differential attraction responses of predators may be attributed to the area to which prey attractants are diffused with a minimum perceptible attraction gradient formed.

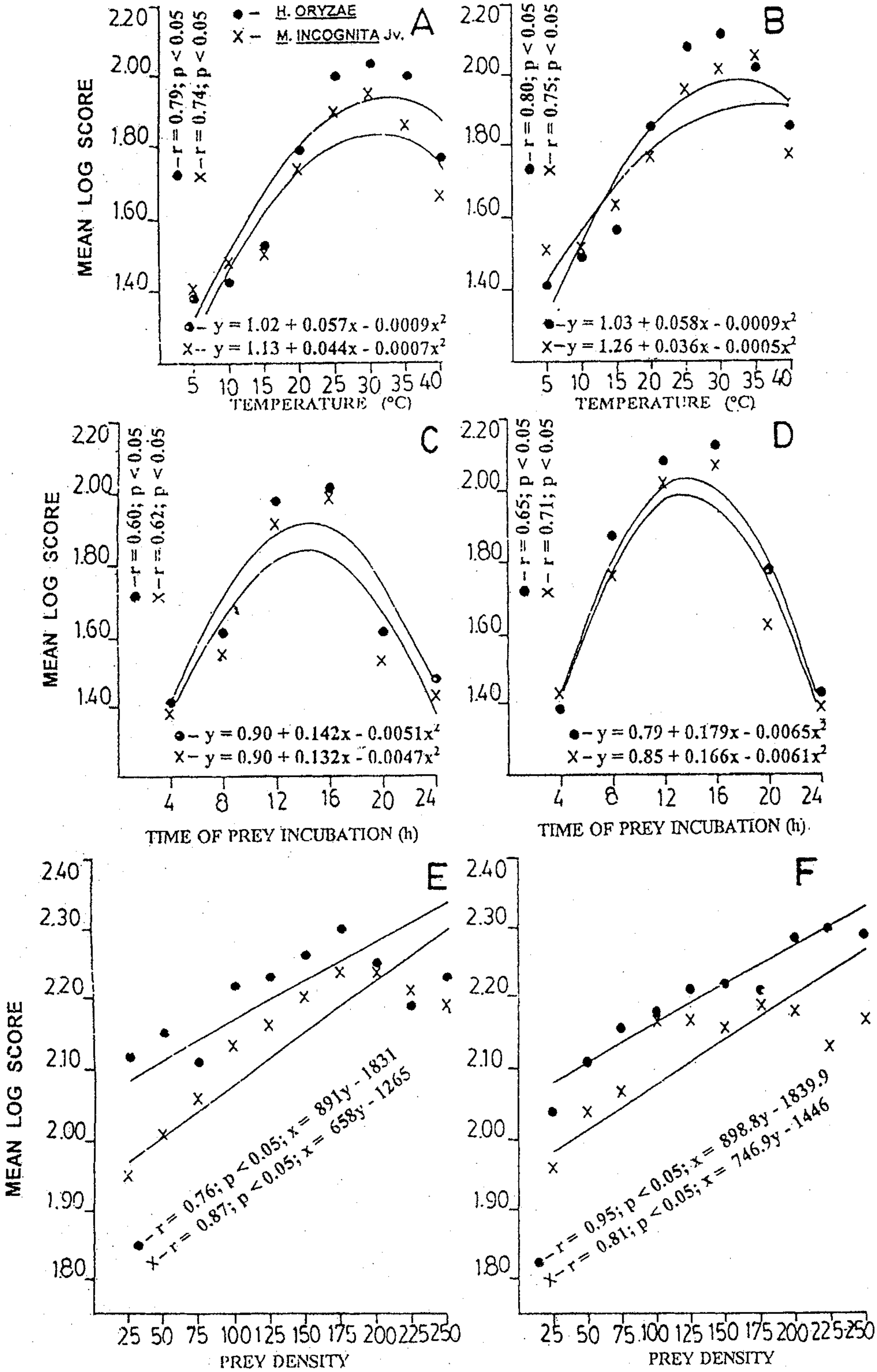

Fig. 1 - Factors influencing attraction of *Mesodorylaimus bastiani*: A = temperature; C = period of prey incubation; E = prey density and of *Aquatides thornei*: B = temperature; D = period of prey incubation; F = prey density.

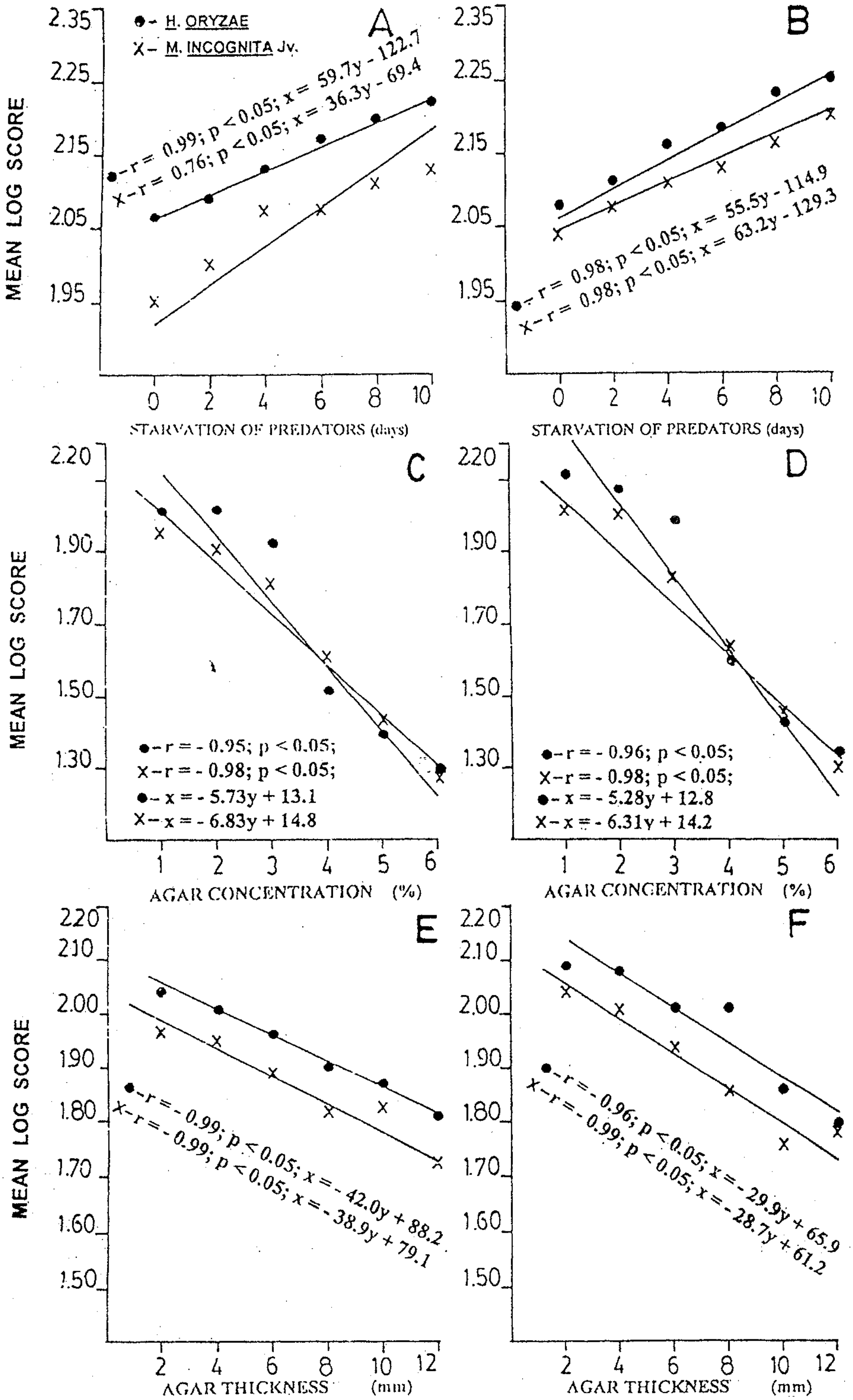

Fig. 2 - Factors influencing attraction of *M. bastiani*: A = period of starvation of predators; C = agar concentration; E = agar thickness and of *A. thornei*: B = period of starvation of predators; D = agar concentration; F = agar thickness.

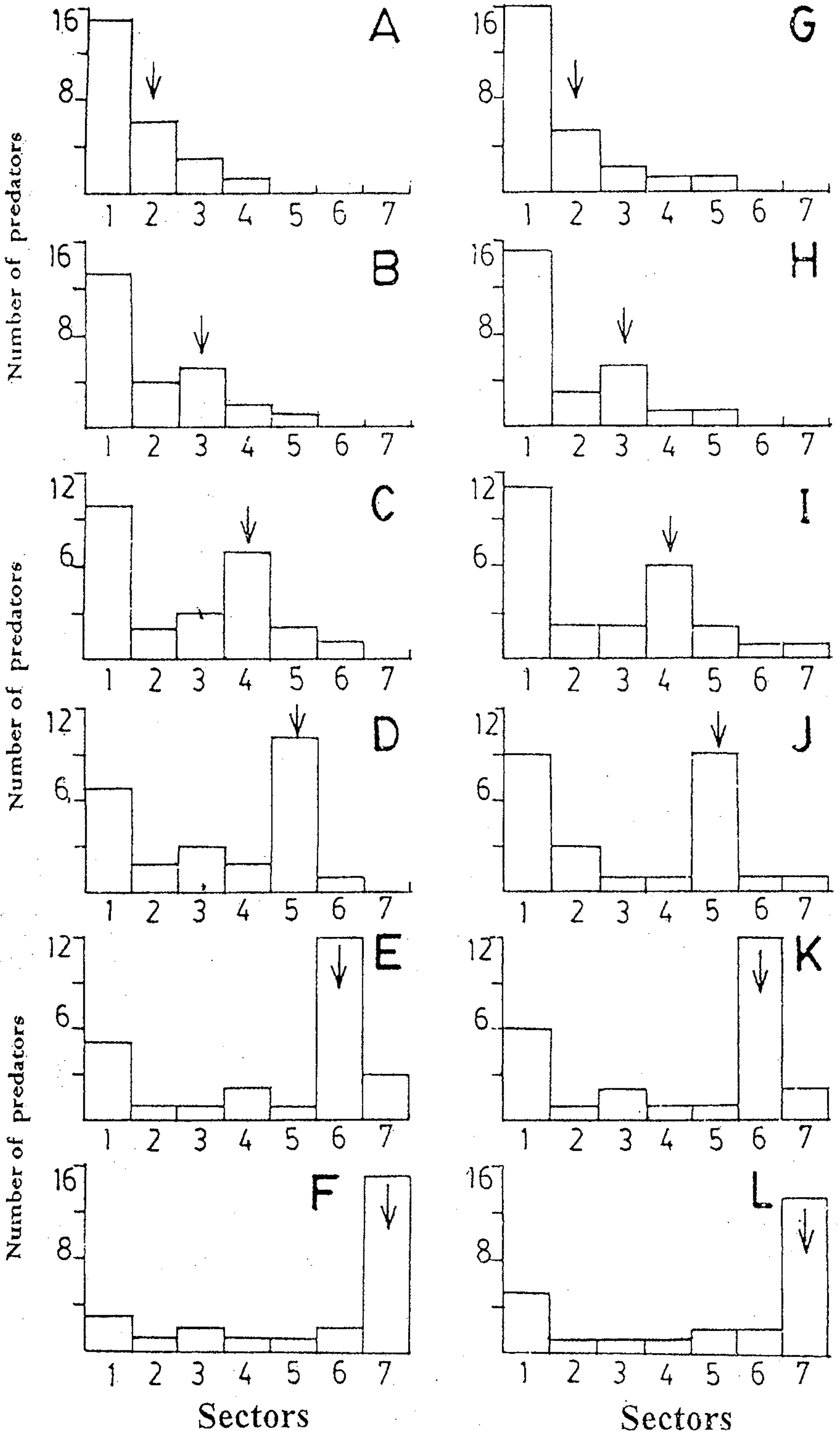

Fig. 3 - Effect of distance of inoculation of *M. bastiani* from prey on their attraction: A-F predators inoculated in sectors 2, 3, 4, 5, 6 and 7 of Petri dishes, respectively, and of *A. thornei* from prey on their attraction: G-L predators inoculated in sectors 2, 3, 4, 5, 6 and 7 of Petri dishes, respectively.

Increase in the distance of inoculation of *M. bastiani* and *A. thornei* from the prey affected their migration towards *H. oryzae* (Fig. 3). Predators responded maximally towards prey when tested from zone 2 and 3 and moderately when tested from other zones.

The attraction of *H. oryzae* (Bilgrami *et al.*, 1985a) and *M. fortidens* and *M. longicaudatus* (Bilgrami and Jairajpuri, 1988) decreased with the increase in their distance of inoculation from the source of attraction. Thus, the phenomenon, observed during present study, could be related to the rate of dispersion of prey attractants and time taken by them to develop a minimum perceptible attraction gradient over increasing distance in a given period of time. The stimuli of stronger intensity only could develop minimum perceptible attraction gradient to elicit minimum response threshold of predators over long distances. Whereas, stimuli of weaker intensities attracted predators only from short distances.

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