Journal of Chemical Ecology, Vol. 19, No. 6, 1993

HOST RECOGNITION BY ENTOMOPATHOGENIC NEMATODES: BEHAVIORAL RESPONSE TO CONTACT WITH HOST FECES

P.S. GREWAL,* R. GAUGLER, and S. SELVAN

Department of Entomology
Rutgers University
New Brunswick, New Jersey 08903

(Received September 14, 1992; accepted February 2, 1993)

Abstract—Host recognition by entomopathogenic nematodes may occur through contact with insects' excretory products, cuticle, or gut contents. We analyzed the behavioral responses of four species of entomopathogenic nematodes during contact with feces of natural or experimental hosts. Host recognition by nematodes was manifested in alterations in the frequency and/or duration of one or more search parameters including forward crawling, head-waving, body-waving, stopping, backward crawling, head-rubbing, and head-thrusting. *Heterorhabditis bacteriophora* and *Steinernema glaseri* showed behavioral responses to contact with feces of their natural hosts, *Spodoptera exigua* (Lepidoptera) and *Popillia japonica* (Coleoptera), and to the experimental hosts, *Acheata domesticus* (Orthoptera) and *Blatella germanica* (Blatteria). *Steinernema carpocapsae* responded only to *B. germanica* feces, whereas *S. scapterisci* did not significantly respond to any of the insect species. During contact with cockroach feces, all nematodes, except *S. scapterisci*, showed avoidance behavior. We suggest that ammonia present in cockroach feces is inhibitory to nematodes. Specific host recognition by entomopathogenic nematodes may be an important mechanism to maintain host affinities.

Key Words—Host recognition behavior, entomopathogenic nematodes, feces, *Spodoptera exigua*, Lepidoptera, Noctuidae, *Popillia japonica*, Coleoptera, Scarabaeidae, *Blattella germanica*, Blatteria, Blattellidae *Acheata domesticus*, Orthoptera, Gryllidae.

INTRODUCTION

Host recognition is a vital step in the life cycle of most parasites. In plant (e.g., Grundler et al., 1991) and animal (e.g., Stewart et al., 1987; Granzer and Haas,

*To whom correspondence should be addressed.

0098-0331/93/0600-1219$07.00/0

1991) parasitic nematodes, host recognition consists of a sequence of behavioral responses to an array of stimuli associated with host or host-related materials. For instance, on exposure to the root exudates of a host plant, second-stage juveniles of *Heterodera schachtii* exhibit a preinfection exploratory behavior that includes stylet thrusting and head-end bending (Grundler et al., 1991). In response to environmental and host stimuli, infective juveniles of the hookworm *Ancylostoma caninum* initiate host-finding and host recognition in four behavioral phases including: snakelike movement, waving behavior, creeping direction, and penetration behavior (Granzer and Haas, 1991).

Entomopathogenic nematodes in the families Steinernematidae and Heterorhabditidae possess tremendous potential as biological control agents of insects (Gaugler and Kaya, 1990). The soil-inhabiting, infective juveniles sense, search for, and invade suitable host insects. Host search by the infective juveniles is believed to include directed orientation towards host-released stimuli, such as CO_2 (Gaugler et al., 1980), excretory products (Schmidt and All, 1978, 1979), and temperature gradients (Pye and Burman, 1981; Byers and Poinar, 1982). Lewis et al. (1992) reported that infective juveniles of *Steinernema glaseri* shifted from ranging to localized search after contact with feces or cuticle of potential host insects. However, host recognition and its specificity in entomopathogenic nematodes is totally unstudied.

Although entomopathogenic nematodes possess an extremely broad laboratory host range (Poinar, 1979), ecological and behavioral barriers restrict their natural host range (Gaugler, 1988). Owing to its sit-and-wait (ambush) host-seeking behavior (Gaugler et al., 1990; Lewis et al., 1992), *S. carpocapsae* is well adapted to parasitize active, surface-dwelling insect species. Conversely, *S. glaseri* is highly mobile (cruiser) and is therefore best adapted to parasitize sedentary, subterranean insect species (Kaya, 1990; Lewis et al., 1992). In field populations, *S. glaseri* is associated with scarabaeid larvae and *S. carpocapsae* with lepidopteran larvae (Poinar, 1990).

Temporal and spatial factors, such as synchronous life cycles and differing habitat preferences, also appear to determine the host range of entomopathogenic nematodes (Webster and Dunphy, 1988). For example, New Zealand populations of *S. feltiae* occur at the bases of tussock grass, where they have become adapted to parasitize lepidopteran larvae (Noctuidae and Hepialidae) feeding on the roots of these grasses (Poinar, 1990). These strains of *S. feltiae* are ineffective parasites of native scarabaeid larvae living in the same habitat. Danish populations of *S. feltiae* have become adapted to parasitize bibionid flies (Bovien, 1937). Another nematode species, *S. scapterisci* Nguyen and Smart, is well adapted to parasitize mole crickets in Uruguay (Nguyen and Smart, 1990).

Although the mechanism of host recognition in entomopathogenic nematodes is not understood, the above examples of host-specific adaptations suggest that specific host recognition occurs. The response to CO_2 by some nematodes

suggests that volatile cues are general attractants, permitting host habitat location, but providing little information about their source. Host recognition in these nematodes may occur through contact with insect (1) excretory products, (2) cuticle, or (3) gut contents. In this paper, we concentrated on host recognition by entomopathogenic nematodes when in contact with insect feces. Behavioral responses of four nematode species to natural and experimental hosts were compared. We consider a natural host as an insect species from which the nematode has been isolated in the field, while experimental hosts are not normally associated with the nematode species in field collections. We hypothesized that if there is specific host recognition, then entomopathogenic nematodes should respond differently to contact cues from the natural versus experimental hosts.

METHODS AND MATERIALS

Entomopathogenic nematode species originally isolated from different groups of insect species (Poinar, 1990) were selected for testing: *S. carpocapsae* from lepidopteran larvae, *S. glaseri* from scarabaeid larvae, *S. scapterisci* from mole crickets, and *Heterorhabditis bacteriophora* from lepidopteran and scarabaeid larvae. Four insect species were chosen to represent the above groups of hosts: the house cricket *Acheata domesticus* (Orthoptera: Gryllidae), the German cockroach *Blatella germanica* (Blatteria: Blattellidae), the Japanese beetle grub *Popillia japonica* (Coleoptera: Scarabaeidae), and the beet armyworm *Spodoptera exigua* (Lepidoptera: Noctuidae).

Nematode Cultures. Infective juvenile *H. bacteriophora* (HP88), *S. carpocapsae* (All), and *S. glaseri* (NC) were cultured in last-instar wax moth (*Galleria mellonella*), at 25°C, following Dutky et al. (1964). *S. scapterisci* (Uruguay) was reared in adult house cricket. All experiments were performed with infective juveniles, harvested three to five days after initial emergence from the host and washed three times in sterile distilled water.

Preparation of Fecal Extracts. Feces were collected from adult house cricket, adult German cockroach, last-instar Japanese beetle, and last-instar beet armyworm reared on their respective diets: house cricket at 25°C, on rabbit food (Blue Seal Foods, Inc., Lawrence, Massachusetts), German cockroach at 27°C on rat chow 5012 (Purina Mills, Inc., St. Louis, Missouri), Japanese beetle at 25°C on roots of turfgrass, and beet armyworm at 28°C on Lima bean (*Phaseolus vulgaris*) leaves. Fifty insects were collected from the cultures and placed individually in well plates (12.5 × 8.5 cm) where they were held for 24 hr at 25°C before the feces were collected. Immediately after collection, 20 mg of feces were mixed with 2 ml of sterile distilled water, macerated, centrifuged at 3000 rpm for 3 min, and the supernatant was collected.

Nematode Behavior Assay. The assay arena was a microscope slide (7.5

× 3.5 cm) covered with a 3-mm layer of 1.5% agar. Immediately before testing, 20 μl of fecal extract was spread uniformly over the agar with a nylon brush. One infective juvenile was then placed on the agar and, after 15 sec of acclimatization to the new surface, its behavior was monitored for 2 min. Only actively moving infective juveniles were chosen. The frequency and duration of forward crawling, head-waving, body-waving, stopping, backward crawling, head-rubbing, and head-thrusting were recorded using a computerized tabulation software (Observer R, Noldus, Wageningen, The Netherlands). The behaviors were defined as follows: (1) forward crawling—sinusoidal forward movement generated by backward body waves; (2) head-waving—lifting <25% of the anterior of the body from the substrate with side-to-side movement; (3) body-waving—lifting 26–75% of anterior of the body with side-to-side movement [this behavior is different from nictation as described by Ishibashi and Kondo (1990), wherein the nematode stands on its tail, almost straight, and waves in the air]; (4) stopping—still, no visible movement for a time span greater than 2 sec; (5) backward crawling—sinusoidal backward movement generated by forward body waves; (6) head-rubbing—pushing of head against the body making a "pea" shape; and (7) head-thrusting—repeated pushing of head against the substrate.

Every nematode species was exposed to fecal extracts from each insect species tested, comprising 16 combinations in all. Fifteen nematodes (replicates) were studied for each treatment. Five nematodes were studied on each of the three slides. Only exsheathed infective juveniles were used. Control slides were treated with 20 μl of sterile distilled water.

Determination of Deterrent in Cockroach Feces. Cockroach feces are known to contain large quantities of ammonia (Mullins and Cocran, 1973); therefore, we determined the quantity of ammonia in the German cockroach feces following Oser (1954). The effects of pure ammonia (derived from ammonium hydroxide, 30% NH_3, Fisher Scientific, Springfield, New Jersey) at the concentration equivalent to that in feces on the behavior of *H. bacteriophora* were evaluated. As ammonia readily dissolves in boric acid, feces were mixed with boric acid to remove ammonia. The effects of feces thus treated with boric acid on behavior of *H. bacteriophora* were studied. One hundred microliters of 4% boric acid (H_3BO_3, Fisher Scientific, Springfield, New Jersey) was mixed with 100 μl of fecal extract prior to its application to the agar surface. Treatment with sterile distilled water and pure ammonia + boric acid served as controls. Only 20 μl of the test solution was applied to the agar surface, and the frequency and duration of various behaviors were recorded as described above.

Statistical Analysis. The relative duration of various behaviors was converted to percent and then normalized using arcsine transformation. The transformed data and the data on frequency of behaviors were analyzed using analysis

of variance and Tukey's studentized range test (SAS Institute, 1982). All comparisons were at the 0.05 significance level.

RESULTS

Response to Extracts from Feces. Heterorhabditis bacteriophora and *S. glaseri* infective juveniles altered their behavior in response to contact with feces of all four insect species (Figures 1–4). When in contact with feces from a member of its natural group of hosts, the beet armyworm, *H. bacteriophora*, significantly reduced the duration of forward crawling and increased the duration and frequency of stopping and head-thrusting (Figure 1). In response to contact with feces from another natural host, the Japanese beetle, *H. bacteriophora* significantly reduced the duration of forward crawling and increased the duration and frequency of head-thrusting. The response of *H. bacteriophora* to contact

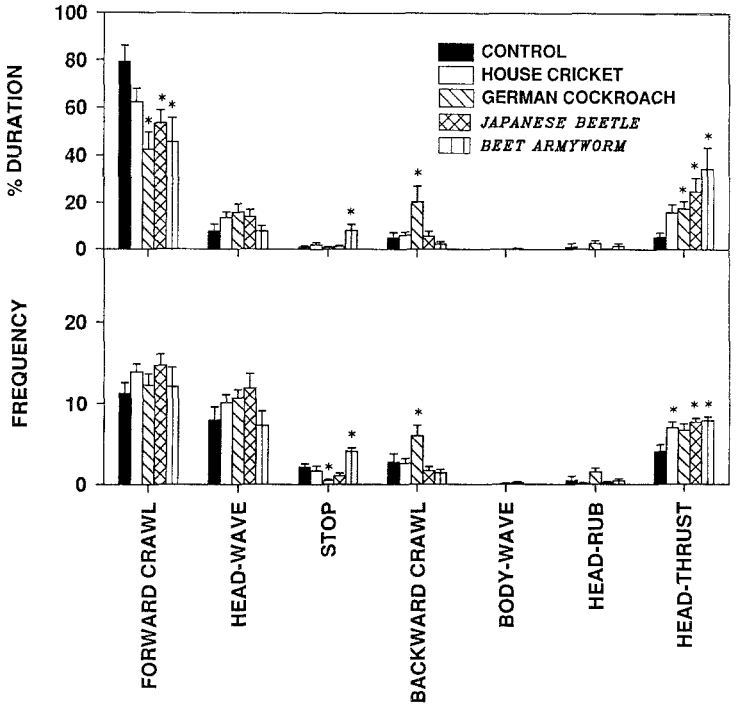

FIG. 1. Duration and frequency (±SE) of various behaviors of *Heterorhabditis bacteriophora* during contact with insect fecal extracts or water. Italicized figure legends represent natural hosts. Asterisks denote values significantly different from controls at 0.05% level.

with feces of the two experimental hosts was different. For example, during contact with feces from the house cricket, *H. bacteriophora* significantly increased only the frequency of head-thrusting, whereas with feces from the German cockroach, the nematodes significantly decreased the duration of forward crawling and increased the duration of backward crawling and the frequency and duration of head-thrusting.

During contact with feces from the natural host, the Japanese beetle, *S. glaseri* significantly reduced the frequency of head-waving and increased the duration and frequency of head-thrusting (Figure 2). Infective juvenile *S. glaseri* also showed different responses to contact with feces of the experimental hosts. For example, during contact with feces from the beet armyworm, *S. glaseri* significantly reduced the duration of forward crawling and increased the duration of head-waving and the frequency and duration of head-thrusting. During contact with feces from the house cricket, *S. glaseri* only significantly increased the frequency and duration of head-thrusting, whereas the nematodes increased the

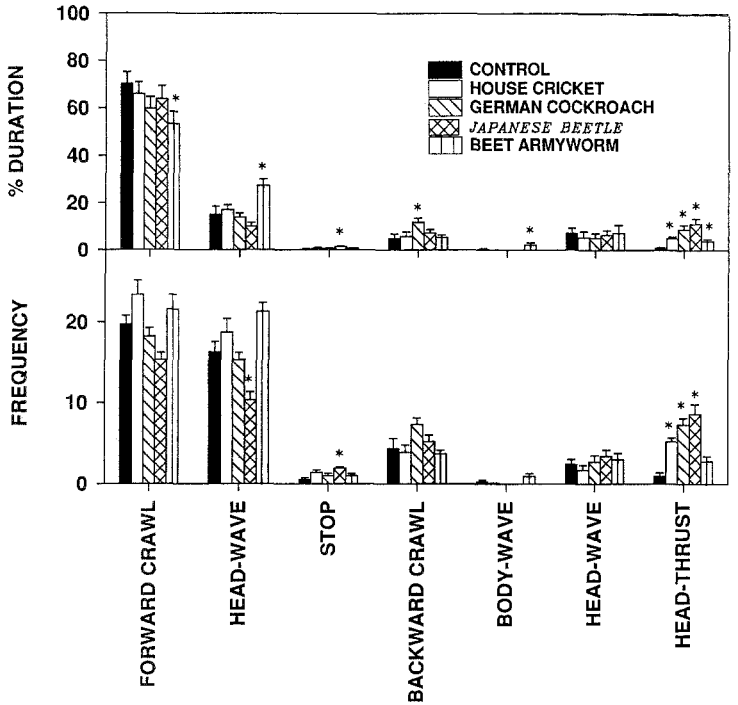

FIG. 2. Duration and frequency (±SE) of various behaviors of *Steinernema glaseri* during contact with insect fecal extracts or water. Italicized figure legends represent natural hosts. Asterisks denote values significantly different from controls at 0.05% level.

duration of backward crawling and frequency and duration of head-thrusting when in contact with feces from the German cockroach.

Infective juvenile *S. carpocapsae* did not show measurable response to contact with feces of their natural hosts (Figure 3). However, the infective juveniles responded to contact with feces of the German cockroach by significantly increasing the frequency and duration of backward crawling. *Steinernema scapterisci* did not significantly respond to feces of any of the insects examined (Figure 4).

Determination of Deterrent in Cockroach Feces. Each milligram of cockroach feces contained 0.9 (±0.02) μl of ammonia. Ammonia at this concentration was inhibitory to *H. bacteriophora* infective juveniles (Figure 5); the nematodes spent 23.5% of the total time backward crawling. The inhibitory effect of ammonia was almost equivalent to that of feces with which nematodes spent about 21.5% of time backward crawling. When boric acid was mixed

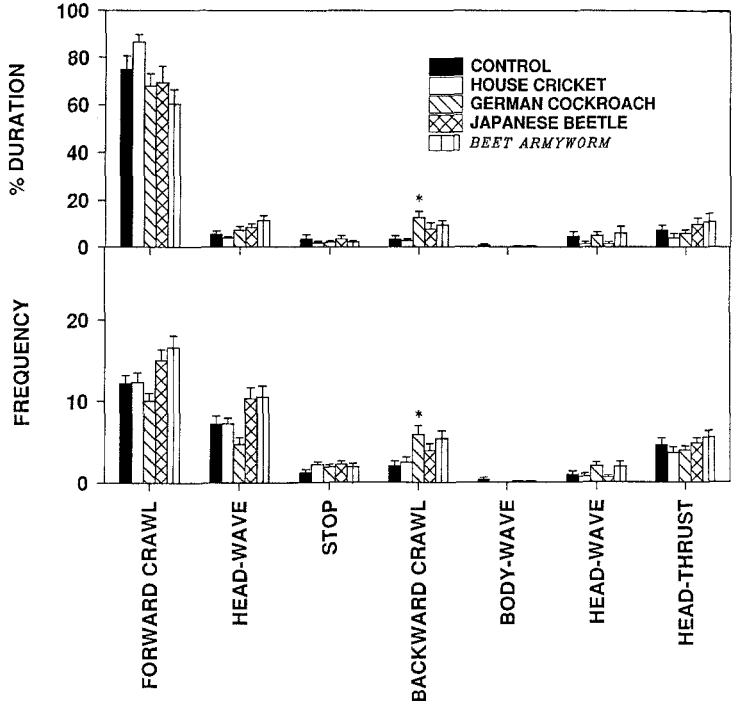

FIG. 3. Duration and frequency (±SE) of various behaviors of *Steinernema carpocapsae* during contact with insect fecal extracts or water. Italicized figure legends represent natural hosts. Asterisks denote values significantly different from controls at 0.05% level.

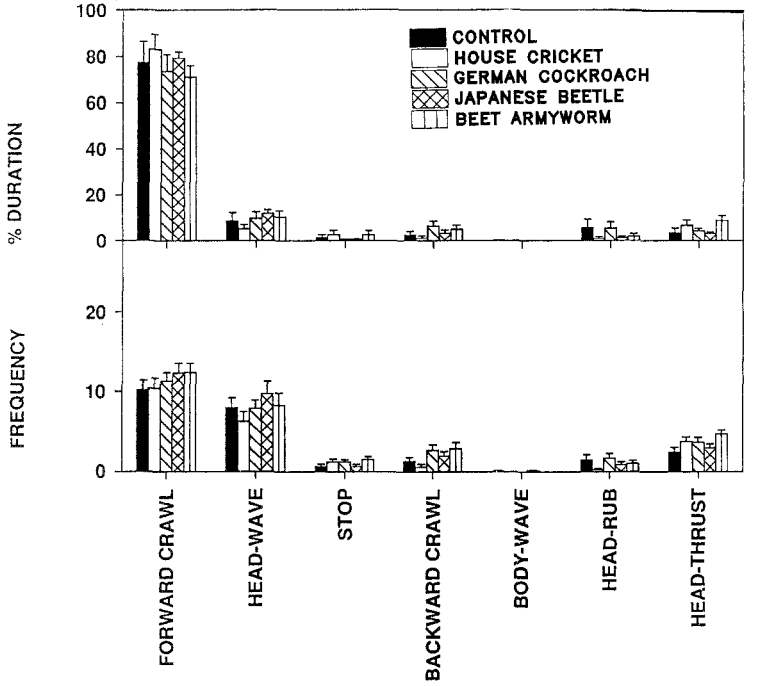

FIG. 4. Duration and frequency (±SE) of various behaviors of *Steinernema scapterisci* during contact with insect fecal extracts or water. Asterisks denote values significantly different from controls at 0.05% level.

with ammonia or fecal extract, the frequency and duration of backward crawling by nematodes did not differ significantly from the control.

DISCUSSION

Not all nematode species altered their behavioral sequence in response to contact with feces from either the natural or experimental hosts. Infective juvenile *H. bacteriophora* and *S. glaseri* changed their behavior in some manner to feces from all four insect species, whereas *S. scapterisci* did not significantly alter its behavior to any of them. *Steinernema carpocapsae* significantly responded to only German cockroach feces. This overall pattern of behavioral modification of nematode species in response to contact cues fits well with their host search behavior. Infective juveniles of *H. bacteriophora* and *S. glaseri* have many of the characteristic behaviors of cruise foragers (Gaugler, 1988), whereas *S. carpocapsae* (Gaugler, 1988) and *S. scapterisci* (Grewal et al.,

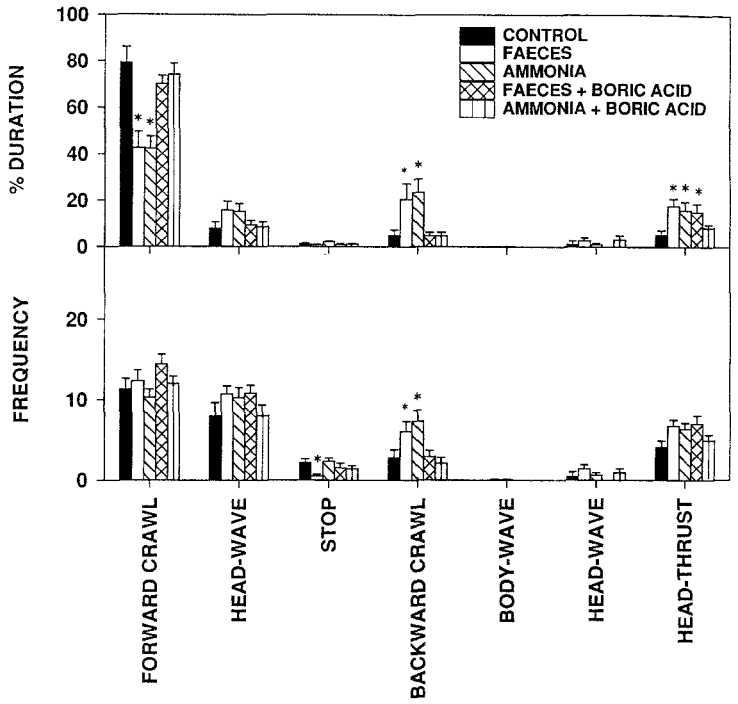

FIG. 5. Effects of fecal extracts of the German cockroach *Blatella germanica* or ammonia on the duration and frequency (±SE) of various behaviors of *Heterorhabditis bacteriophora*. Boric acid was used to absorb ammonia. Asterisks denote values significantly different from controls at 0.05% level.

1993a) are ambush foragers. The relevance of chemical cues in host search by the two types of foragers differ: cruising foragers rely more heavily on chemical cues than ambush foragers (Bell, 1991). In another study, *S. glaseri* responded to selected host cues by shifting from ranging to localized search, characterized by decreased locomotory rate, distance traveled, search area, and the proportion of the test period spent moving, whereas *S. carpocapsae* did not measurably respond to the same host cues (Lewis et al., 1992). Furthermore, *S. carpocapsae* and *S. scapterisci* infective juveniles use an alternative mechanical means of attachment to the host, nictation (Campbell and Gaugler, 1993) and therefore, are less likely to be affected by chemical host cues. Our results further support that cruiser nematode species respond more strongly to the chemical host cues (feces) than the ambush foragers.

Infective juveniles of *H. bacteriophora* and *S. glaseri* exhibited specific behavioral changes after contact with feces of the four insect species examined.

For example, when in contact with feces of the natural host, the beet armyworm, infective juvenile *H. bacteriophora* reduced the time spent forward crawling and increased the frequency and duration of stopping and head-thrusting, whereas with the experimental host, the house cricket, the nematodes increased the duration and frequency of head-thrusting only. *S. glaseri* decreased the frequency of head-waving and increased the duration and frequency of head-thrusting during contact with feces of the natural host, the Japanese beetle, whereas the nematodes reduced the duration of forward crawling and increased the frequency and duration of head-waving and head-thrusting with feces from the experimental host, the beet armyworm. These host-specific alterations in nematode behavior during contact with feces suggest host recognition by entomopathogenic nematodes.

Host affinities seen in field populations have been attributed to ecological similarity and behavioral compatibility between nematodes and their respective host species of insects (Webster and Dunphy, 1988). For example, subterranean insects are unlikely to be parasitized by surface-foraging nematodes, and ambush foragers would rarely encounter sedentary hosts. In addition to ecological mechanisms and search strategies reinforcing the recognized host–parasite pairs, however, there is evidence that *S. glaseri* shifts from ranging to localized search more strongly after contact with feces from their natural host, the Japanese beetle, than with feces from the beet armyworm (Lewis et al., 1992). Our study confirms this observation and supports host recognition as an important mechanism to maintain host affinities of entomopathogenic nematodes.

When in contact with cockroach feces, all the nematode species except *S. scapterisci* significantly increased the frequency and time spent backward crawling. Mixing of cockroach feces with boric acid, which absorbed ammonia, eliminated the backward crawling behavior of *H. bacteriophora*, suggesting that the ammonia present in the feces was inhibitory. Pye and Burman (1981) reported that ammonia at 7.5 mM concentration repelled *S. carpocapsae*. Zervos and Webster (1989) reported that the American cockroach *Periplaneta americana* is not very susceptible to parasitism by *Heterorhabditis zealandica* (= *Heterorhabditis heliothidis* T327); nymphs were only parasitized when forced into prolonged exposure to a damp substrate rich in nematodes, and adults when starved and dehydrated. Cockroaches being externally ammonotellic (Bell and Adiyodi, 1981), excrete ammonia as the major nitrogenous material in feces. The avoidance behavior of nematodes in the presence of ammonia may restrict nematode penetration through the anus from which ammonia is excreted. This may have important implications in the biological control of cockroaches with entomopathogenic nematodes.

Sensitivity of *H. bacteriophora* to contact with German cockroach feces was related to the ineffective parasitism of cockroaches by the nematodes (Grewal et al., 1993b). However, *S. scapterisci* did not show a significant increase

in backward crawling during exposure to cockroach feces, and they effectively parasitized adult cockroaches. The lesser sensitivity of *S. scapterisci* to contact with the German cockroach feces may be due to its adaptation to parasitize cockroaches (Grewal et al., 1993b).

Another interesting aspect of the interaction between nematodes and cockroach feces or ammonia was the increase in the duration of head-thrusting. Besides negative locomotion, *H. bacteriophora* significantly increased the duration of head-thrusting while in contact with ammonia. In the presence of a toxic bacterium, *Bacillus* sp., the free-living nematode *Caenorhabditis elegans* frequently burrowed into the nutrient agar substrate (Grewal, 1990). Although the nematodes were unable to burrow into the 1.5% plain agar we used, the increase in head-thrusting was associated with the increase in nematode reversals. Therefore, the increased head-thrusting may be a part of the nematodes' behavioral repertoire representing avoidance.

The present study has recorded the scanning behaviors of entomopathogenic nematodes in the presence or absence of host excretory products. Scanning is the set of mechanisms by which animals move their receptors and sometimes their bodies or appendages to capture information from the environment efficiently (Evans and O'Brian, 1986). Some insects locate resources by casting their bodies or appendages to the left and right of the path, thereby increasing the arc within which prey can be contacted laterally, e.g., larvae of nectivorous flies (Syrphidae) and lacewings (Chrysopidae) (Bansch, 1966; Chandler, 1969). Nematode attraction to chemical stimuli has often been attributed to klinotactic orientation (Croll, 1970; Dusenberry, 1980, 1983). The side-to-side movements or head-waving of nematodes has been interpreted as sampling stimuli (Gaugler et al., 1980; Green, 1980). Presumably the distance between the amphids is insufficient to permit comparison of the intensity of stimulation without head movement (Wharton, 1986; Ishibashi and Kondo, 1990). Apparently other behaviors including body-waving, frequency of stops (stopping), backward crawling, head-rubbing, and head-thrusting also constitute a nematode's host-scanning mechanism. Although the significance of all the individual behaviors is not yet known, host-specific alterations in nematode behavioral responses suggest specific host recognition by entomopathogenic nematodes.

Acknowledgments—We thank James Campbell for technical help and Edwin Lewis for critical review of the manuscript. This research was supported in part by the Turf Grass Fund. This article is New Jersey Agricultural Experiment Station Publication No. D-08255-12-92, supported by state funds and the U.S. Hatch Act.

REFERENCES

BANSCH, R. 1966. On prey-seeking behavior of aphidophagous insects, pp. 123–128, *in* I. Hodek (ed.). Proceedings of the Prague Symposium on Ecology of Aphidophagous Insects. Academia, Prague.

BELL, W.J. 1991. Searching Behaviour: The Behavioural Ecology of Finding Resources (Animal Behaviour Series). Chapman and Hall, London.

BELL, W.J., and ADIYODI, K.G. 1981. The American Cockroach. Chapman and Hall, London.

BOVIEN, P. 1937. Some types of association between nematodes and insects. *Vidensk. Medd. Dan. Naturhist. Foren. Khobenhavn* 101:1–114.

BYERS, J.A., and POINAR, G.O., JR. 1982. Location of insect hosts by the nematode *Neoplectana carpocapsae* in response to temperature. *Behavior* 79:1–10.

CAMPBELL, J.F., and GAUGLER, R. 1993. Nictation behavior and its ecological implications in entomopathogenic nematode search strategies. *Behaviour* In press.

CHANDLER, A.E.F. 1969. Locomorory behavior of first instar larvae of *Aphidophagous syrphidae* (Diptera) after contact with aphids. *Anim. Behav.* 17:673–678.

CROLL, J. 1990. The Behavior of Nematodes: Their Activity, Senses and Responses. Edward Arnold, London.

DUSENBERRY, D.B. 1980. Behavior of free-living nematodes, pp. 127–158, *in* B.M. Zukerman (ed.). Nematodes as Biological Models. Academic Press, New York.

DUSENBERRY, D.B. 1983. Chemotactic behavior of nematodes. *J. Nematol.* 15:168–173.

DUTKY, S.R., THOMPSON, J.V., and CANTWELL, G.E. 1964. A technique for the mass propagation of the DD-136 nematode. *J. Insect Pathol.* 6:417–422.

EVANS, B.I., and O'BRIAN, W.J. 1986. An analysis of the feeding rate of white crappie. *Develop. Environ. Biol. Fish.* 7:200–306.

GAUGLER, R. 1988. Ecological considerations in the biological control of soil-inhabiting insects with entomopathogenic nematodes. *Agric. Ecosys. Environ.* 24:351–360.

GAUGLER, R., and KAYA, H.K. 1990. Entomopathogenic Nematodes in Biological Control. CRC Press, Boca Raton, Florida.

GAUGLER, R., LEBECK, L., NAKAGAKI, B., and BOUSH, G.M. 1980. Orientation of the entomopathogenic nematode *Neoaplectana carpocapsae* to carbon dioxide. *Environ. Entomol.* 9:649–652.

GAUGLER, R., CAMPBELL, J.F., and MCGUIRE, T. 1990. Selection for host finding in *Steinernema feltiae*. *J. Invertebr. Pathol.* 54:363–372.

GRANZER, M., and HAAS, W. 1991. Host-finding and host recognition of infective *Ancylostoma caninum* larvae. *Int. J. Parasitol.* 21:429–440.

GREEN, C.D. 1980. Nematode sex attractants. *Helminthol. Abstr.* 49B:81–93.

GREWAL, P.S. 1990. Studies on saprobic rhabditid nematodes and their associated bacteria affecting mushroom culture. PhD thesis. University of London.

GREWAL, P.S., GAUGLER, R., KAYA, H.K., and WUSATY, M. 1993a. Infectivity of the entomopathogenic nematode *Steinernema scapterisci* (Nematoda: Steinernematidae). *J. Invertebr. Pathol.* In press.

GREWAL, P.S., GAUGLER, R., and LEWIS, E.E. 1993b. Host recognition behavior of entomopathogenic nematodes during contact with gut contents. *J. Parasitol.* 77:In press.

GRUNDLER, F., SCHNIBBE, L., and WYSS, U. 1991. In vitro studies on the behavior of second-stage juveniles of *Heterodera schachtii* (Nematoda: Heteroderidae) in response to host plant root exudates. *Parasitology* 103:149–155.

ISHIBASHI, N., and KONDO, E. 1990. Behavior of infective juveniles, pp. 139–150, *in* R. Gaugler and H.K. Kaya (eds.). Entomopathogenic Nematodes in Biological Control. CRC Press, Boca Raton, Florida.

KAYA, H.K. 1990. Soil ecology, pp. 93–117, *in* R. Gaugler and H.K. Kaya (eds.). Entomopathogenic Nematodes in Biological Control. CRC Press, Boca Raton, Florida.

LEWIS, E.E., GAUGLER, R., and HARRISON, R. 1992. Entomopathogenic nematode host finding: Response to host contact cues by cruise and ambush foragers. *Parasitology* 105:309–315.

MULLINS, D.E., and COCHRAN, D.G. 1973. Nitrogenous excretory materials from the American cockroach. *J. Insect Physiol.* 19:1007–1018.

NYUGEN, K.B., and SMART, G.C., JR. 1990. *Steinernema scapterisci* n. sp. (Rhabditida: Steinernematidae). *J. Nematol.* 22:187–199.

OSER, B.L. 1954. Hawk's Physiological Chemistry, 14th ed. McGraw-Hill, New York.

POINAR, G.O., JR. 1979. Nematodes for Biological Control of Insects. CRC Press, Boca Raton, Florida.

POINAR, G.O., JR. 1990. Taxonomy and biology of Steinernematidae and Heterorhabditidae, pp. 23–61, *in* R. Gaugler and H.K. Kaya (eds.). Entomopathogenic Nematodes in Biological Control. CRC Press, Boca Raton, Florida.

PYE, A.E., and BURMAN, M. 1981. *Neoaplectana carpocapsae*: Nematode accumulations on chemical and bacterial gradients. *Exp. Parasitol.* 51:13–20.

SAS INSTITUTE. 1982. SAS User's Guide: Statistics. SAS Institute, Cary, North Carolina.

SCHMIDT, J., and ALL, J.N. 1978. Chemical attraction of *Neoaplectana carpocapsae* (Nematoda: Steinernematidae) to insect larvae. *Environ. Entomol.* 7:605–607.

SCHMIDT, J., and ALL, J.N. 1979. Attraction of *Neoaplectana carpocapsae* (Nematoda: Steinernematidae) to common excretory products of insects. *Environ. Entomol.* 8:55–61.

STEWART, G.L., DESPOMMIER, D.D., BURNHAM, J., and RAINES, K.M. 1987. *Trichinella spiralis*: Behavior, structure, and biochemistry of larvae following exposure to components of the host enteric environment. *Exp. Parasitol.* 63:195–204.

WEBSTER, J.M., and DUNPHY, G.B. 1988. Host compatibility of insects to nematodes, pp. 237–245, *in* J.A. Veech and D.W. Dickson (eds.). Vistas on Nematology: A Commemoration of the Twenty-fifth Anniversary of the Society of Nematologists. Society of Nematologists, Inc., Hyattsville, Maryland.

WHARTON, D.A. 1986. A Functional Biology of Nematodes. The Johns Hopkins University Press, Baltimore, Maryland.

ZERVOS, S., and WEBSTER, J.M. 1989. Susceptibility of cockroach *Perilaneta americana* to *Heterorhabditis heliothidis* (Nematoda: Rhabditoidea) in the laboratory. *Can. J. Zool.* 67:1609–1611.