

**FORAGING BEHAVIOR OF TWO SPECIES OF THE GENUS
CHILOCORUS (COCCINELLIDAE: COLEOPTERA):
A COMPARATIVE STUDY**

H. PODOLER and J. HENEN*

The searching behavior of two coccinellid beetles of the genus *Chilocorus* (Coccinellidae: Coleoptera) was compared. The main components of the searching behavior of larvae and adults – speed of search and change of angle before and after successful encounter with hosts – were compared within and between species. Both species (at the larval and adult stages) changed their searching behavior following successful encounter, by increasing the angle and number of turns per unit of time. These changes were coupled with reductions in the speed of locomotion. The intensity of the changes differed significantly between the species. *C. bipustulatus* demonstrated a stronger response in the degree of change in angle than *C. kuwanae*. As time elapsed and unsuccessful search continued, the beetles returned to their original pattern of search. Both species allocated an increasing proportion of their time to patches of hosts, in accordance with host density.

KEY WORDS: Coccinellidae; *Chilocorus bipustulatus*; *Chilocorus kuwanae*; foraging behavior.

INTRODUCTION

The searching strategy of predators and the time they allocate to searching for prey are currently the subjects of extensive study. The different tactics used by various insect predator species have been described by several authors (e.g. 6,9,12,21, 25). The reports are based on the optimal foraging theory, which assumes that the time allotted by a predator will result in a maximal rate of successful encounters with prey. A comprehensive review on foraging strategies of insects was provided by Hassell and Southwood (11).

A predator (as well as a parasite) might first exhibit a high rate of search activity (number of position changes) at all prey densities. Then it will switch to a different

Received July 9, 1985; received in final form Nov. 20, 1985.

*Dept. of Entomology, The Hebrew University of Jerusalem, Faculty of Agriculture, Rehovot, Israel.

strategy (for example, from pursuance to an ambush strategy), in response to prey density (9). Such response is related to the ability of the predator (or parasite) to gather information from its environment about the relative profitability of the patch within the host habitat (21).

Predator searching behavior can be divided into several stages which include a search for the prey habitat followed by a search between and within the patches of the prey (25). A predator's searching behavior is assumed to change following its initial contact with a prey, and the change is manifested as an increase in the turning rate (= klinokinesis) coupled with a reduction in the speed of movement (= orthokinesis) (16).

In the present study we compare the particular foraging behavior of two coccinellid species (Coleoptera: Coccinellidae) belonging to the genus *Chilocorus*. Coccinellid beetles are known to use some chemical cues effective only at a short distance (23) and to detect their prey only by physical contact (e.g. 1,2,8,22). Thus, locomotory patterns are the crucial mechanism by which the predator's rate of prey contact is determined. The species studied herein are: *Chilocorus bipustulatus* L., a species endemic to the Middle East and considered to be important in reducing the populations of armoured scale insects (Diaspididae) and of some soft scale insects (Coccidae) in citrus groves; and *C. kuwanae* Silvestri, an exotic species introduced into Israel from Japan and considered efficient against various diaspidid scale species in Japan. *C. kuwanae* has not become established in Israel, in part, we suspect, because of its intolerance of the high temperatures prevalent in this region (18).

A comparative study was therefore conducted to examine whether these two predator species exhibit both klinotactic and orthokinetic responses following initial prey contact and, if so, whether the species differ in the pattern in which their behavior is expressed.

MATERIALS AND METHODS

Predatory beetles

The stock culture of *C. bipustulatus* was started from adults collected in citrus groves located in the coastal plain of Israel (Tel Mond area) in 1980. Care was taken to ensure that only beetles free of the parasitic fungus *Hesperomyces virescens* Thaxter (13) were used. The stock culture of the Japanese species *C. kuwanae* was started from beetles received from the Israel Cohen Institute of Biological Control at Rehovot. The original culture in Israel was started from beetles sent by Dr. K. Nohara from Hagi (Japan) in 1976.

The cultures were maintained in separate wooden cages (30 x 40 x 30 cm). Each cage had a glass roof, an open side covered with cloth for ventilation and a side with a hole for a cloth sleeve through which all necessary manipulations were carried out. Diaspidid scale insects, in surplus (on squashes), served as food for the predatory beetles. Flannel strips were placed in the cages as an ovipositional substrate for *C. bipustulatus* (17). Strips of sponge were found, during the present study, to serve the

same purpose for *C. kuwanae*. The cultures were maintained at $27\pm 1^{\circ}\text{C}$, 65% RH, and 16:8 LD. This photoperiod regime prevented the adults from entering into imaginal diapause.

Host cultures

The following diaspidid scale insects served as prey for the predators: the California red scale, *Aonidiella aurantii* (Mask.), the Florida red scale, *Chrysomphalus aonidum* (L.), and the oleander scale, *Aspidiotus nerii* Bouché. Cultures of the prey species were maintained on butternut squash under environmental conditions similar to those of the predators, but in separate rooms.

Searching behavior

The beetle's searching behavior was studied in plastic containers (31 x 24 x 8 cm). Ten prey insects (*A. nerii*) were fastened with a drop of water, in a random manner, to a glass plate (30 x 23 cm) that served as the experimental arena. The glass plate was then placed at the bottom of the plastic container and a sheet of white paper was placed under the experimental arena to provide an optically suitable background. The container was covered with a second glass plate. The plastic container was then placed inside a large wooden cage covered with Styrofoam (for thermal insulation) and containing two fluorescent 15 w lamps for illumination and keeping the temperature within the cage almost constant ($27\pm 1^{\circ}\text{C}$). The searching behavior of the

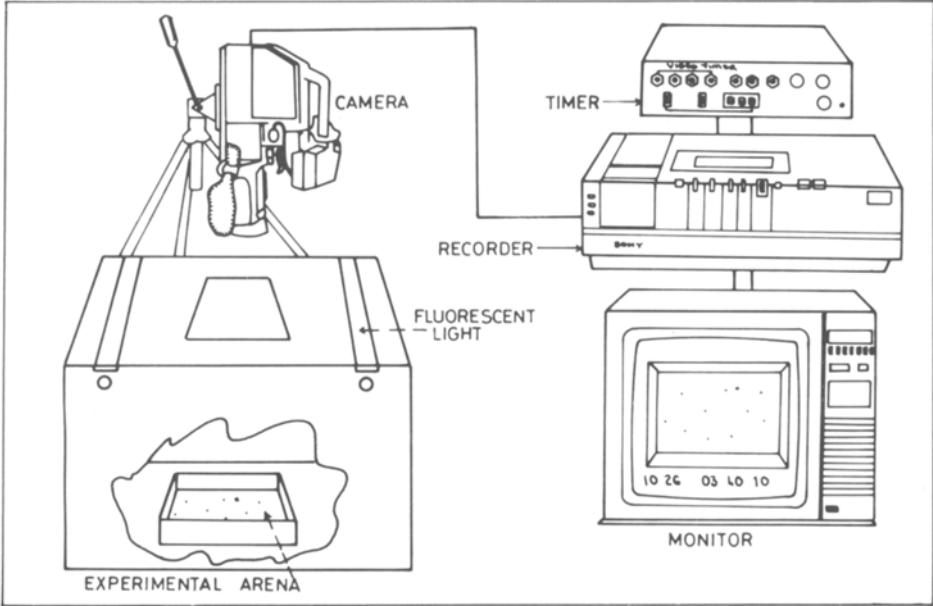


Fig. 1. The system used to record the foraging behavior of the predators.

predators was recorded with a Sony MF Tricon color video camera HVC-2000P connected to a Sony Betamax SL-C7E video recorder with a digital video timer VTG-33 (Fig. 1).

An experiment was initiated when a single 4th-instar larva (= last larval stage) or adult beetle was introduced into the experimental arena. To elicit searching behavior, adult beetles were starved for 24 h prior to their introduction. This was unnecessary with the larvae. Searching behavior recorded in the absence of prey served as the control. Each experiment lasted 3 h and each treatment was replicated ten times.

Analysis of the beetle tracks

The beetles' tracks were drawn on tracing paper attached to the TV screen. The distance traveled during fixed time intervals (10 sec for adults, 20 sec for larvae) was measured using a cartographer's wheel. Tangents were drawn at every turning point and turning angles greater than 5° were measured with a protractor (Fig. 2).

The following parameters were used: the number of turns, the total number of degrees turned, the average number of degrees turned, the degree of angle change per centimeter (obtained by dividing the total number of degrees turned by the distance covered during the same time interval) and the rate of search (distance covered) during the time intervals mentioned above.

A complementary method used to demonstrate the predator's searching racks consisted of analyzing the frequency distribution of the angles turned for each time interval. The angles were classified as belonging to groups: less than 10° (Group O), $11-30^\circ$ (Group 1), $31-50^\circ$ (Group 2), etc. Right turns were recorded as positive values, and left turns as negative values.



Figs. 2. An example of a predator track before and after encounter with a host. The black dot indicates the location where the encounter occurred. The arrows indicate the direction of the track and the vertical lines indicate 10-sec intervals. The numbers represent the distance (in cm). The method used to measure angles turned is demonstrated only on part of the track.

Behavioral response

A predator's response to different host densities was investigated by arranging the host patches (each of *ca* 2 cm²) at four densities: 4, 8, 10 and 24 hosts/patch. The time allocated by the predators to each patch was recorded.

RESULTS

Table 1 summarizes the results obtained for the adults and larvae of the two *Chilocorus* species.

TABLE 1

AN INTRASPECIFIC COMPARISON OF THE FORAGING BEHAVIOR OF *CHILOCORUS BIPUSTULATUS* AND *CHILOCORUS KUWANAE*

(Data analyzed applying ANOVFT on a CDC Cyber 74 computer)

<i>Species and stage</i>	<i>Treatment</i>	<i>Mean change in angle (degrees / cm, ± SD)</i>	<i>Mean speed (cm/sec, ± SD)</i>	<i>Mean number of turns (±SD)</i>
<i>C. bipustulatus</i> , adult	Control (no prey)	26.00 ± 26.45 a**	0.80 ± 0.28 a	6.80 ± 2.81 a
	1st 10 sec*	116.57 ± 61.45 b	0.37 ± 0.15 b	7.93 ± 3.43 a
	2nd 10 sec	70.43 ± 35.07 c	0.43 ± 0.18 b	7.97 ± 3.75 a
	3rd 10 sec	61.43 ± 36.46 c	0.48 ± 0.20 b	7.43 ± 3.47 a
<i>C. kuwanae</i> , adult	Control	26.71 ± 31.14 a	0.72 ± 0.28 a	6.10 ± 1.20 a
	1st 10 sec	97.14 ± 37.47 b	0.58 ± 0.11 b	9.20 ± 2.01 b
	2nd 10 sec	68.00 ± 30.37 c	0.76 ± 0.16 a	9.60 ± 1.94 b
	3rd 10 sec	54.43 ± 20.24 c	0.74 ± 0.14 a	7.90 ± 2.01 b
<i>C. bipustulatus</i> , larval	Control	34.43 ± 23.72 a	0.52 ± 0.34 a	3.00 ± 4.05 a
	1st 20 sec	80.28 ± 44.94 b	0.30 ± 0.38 b	5.60 ± 4.00 b
	2nd 20 sec	59.71 ± 49.85 c	0.35 ± 0.42 b	5.47 ± 3.85 b
	3rd 20 sec	52.43 ± 48.48 ac	0.36 ± 0.39 b	5.43 ± 3.42 b
<i>C. kuwanae</i> , larval	Control	30.43 ± 16.04 a	0.27 ± 0.15 a	2.70 ± 1.15 a
	1st 20 sec	78.57 ± 27.64 b	0.20 ± 0.13 a	3.70 ± 1.74 a
	2nd 20 sec	55.71 ± 30.52 b	0.19 ± 0.10 a	3.47 ± 1.72 a
	3rd 20 sec	55.86 ± 25.62 b	0.21 ± 0.11 a	3.70 ± 1.82 a

*Periods following contact with host (prey).

**Within columns and species groups, numbers followed by different letters are significantly different at $P < 0.05$ (Duncan's Multiple Range Test).

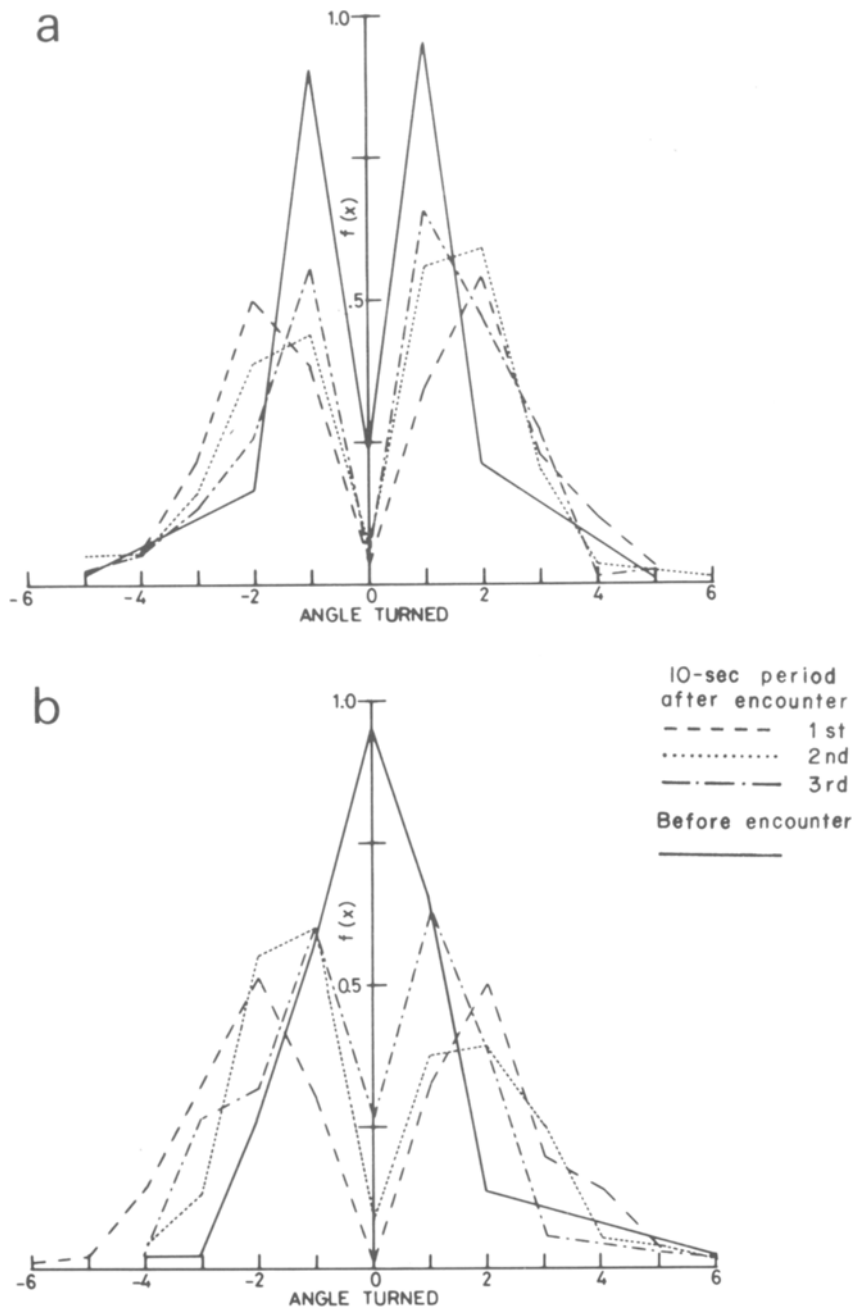


Fig. 3. Frequency distribution of the angles turned by adults of *Chilocorus bipustulatus* (a) and *Chilocorus kuwanae* (b).

TABLE 2

AN INTERSPECIFIC COMPARISON OF THE FORAGING BEHAVIOR OF *CHILOCORUS BIPUSTULATUS* AND *CHILOCORUS KUWANAE*

(Data from Table 1 analyzed applying ANOVFT on a CDC Cyber 74 computer)

Treatment	Species and stage	Mean change in angle (deg/cm)	Mean speed (cm/sec)	Mean number of turns
Control	<i>C. bipustulatus</i> , adult	a**	a	a
	<i>C. kuwanae</i> , adult	a	a	a
	<i>C. bipustulatus</i> , larval	a	b	b
	<i>C. kuwanae</i> , larval	a	c	b
First period*	<i>C. bipustulatus</i> , adult	a	a	a
	<i>C. kuwanae</i> , adult	b	b	a
	<i>C. bipustulatus</i> , larval	b	ac	b
	<i>C. kuwanae</i> , larval	b	c	c
Second period	<i>C. bipustulatus</i> , adult	a	a	a
	<i>C. kuwanae</i> , adult	a	b	b
	<i>C. bipustulatus</i> , larval	a	a	c
	<i>C. kuwanae</i> , larval	a	c	d
Third period	<i>C. bipustulatus</i> , adult	a	a	a
	<i>C. kuwanae</i> , adult	a	b	a
	<i>C. bipustulatus</i> , larval	a	a	b
	<i>C. kuwanae</i> , larval	a	c	c

*Periods lasted 10 and 20 seconds for adults and larvae, respectively.

**Within columns and periods, different letters indicate significant difference at $P < 0.05$ (Duncan's Multiple Range Test).*Adults*

Prior to contacting a prey, both *C. bipustulatus* and *C. kuwanae* adults searched for prey at similar speeds (approx. 0.75 cm/sec), number of turns (approx. 6.5 turns/10 sec) and degree of change in angle (approx. 26.5° /cm). Although the adults turned frequently, the small change in angle indicates that their deviations from the direction of search are relatively slight. This behavior enables the beetles to maintain high speed and cover a large area within the experimental arena.

Adult searching behavior for both species changed significantly following a successful host encounter. The degree of change in angle and the number of turns increased, thereby decreasing the speed of movement significantly (Table 1). With increasing time after leaving the prey, behavior gradually reverted to the searching pattern exhibited prior to the encounter with the first prey.

The two species differed significantly in their behavior after a successful prey encounter. *C. bipustulatus* responded more vigorously, by increasing the angle of

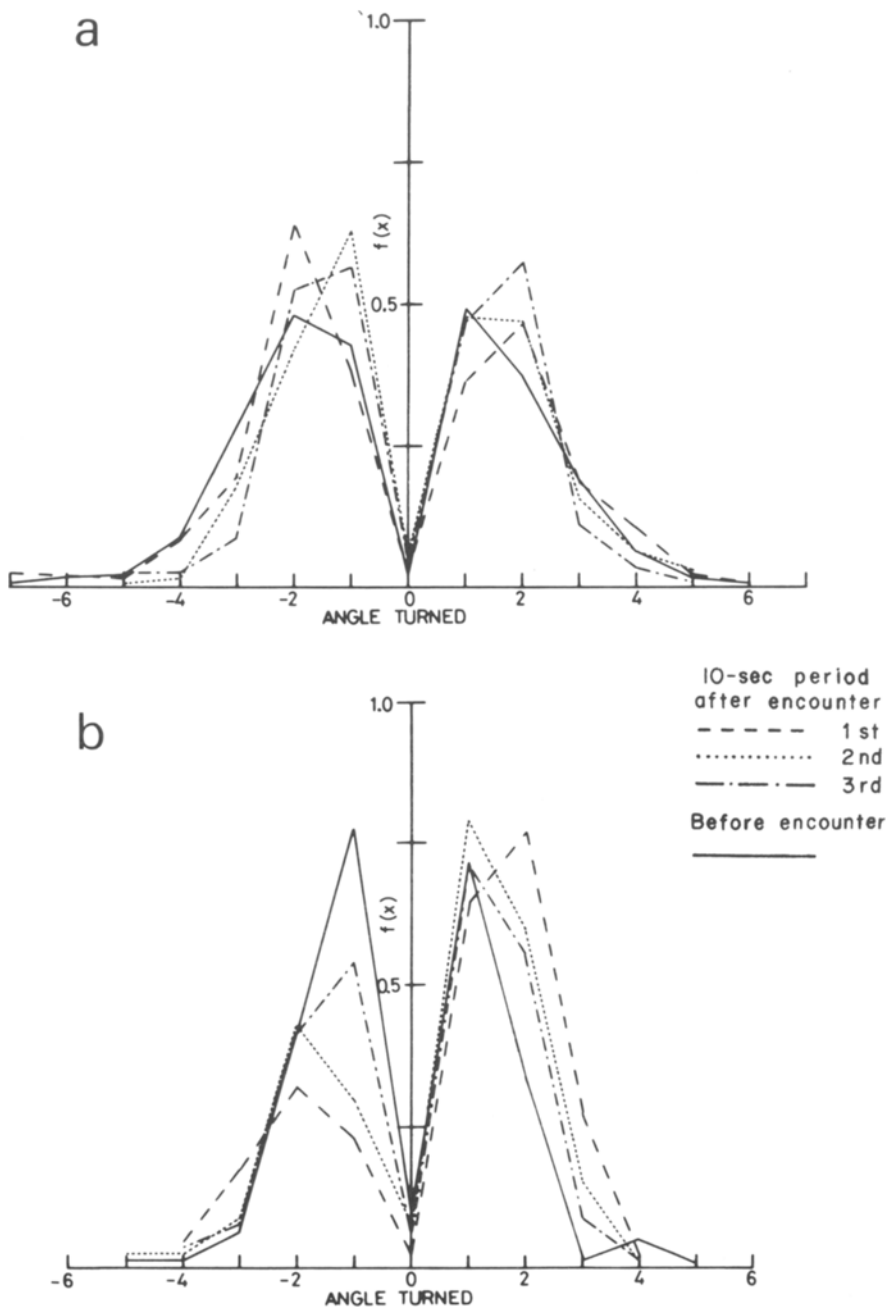


Fig. 4. Frequency distribution of the angles turned by larvae of *Chilocorus bipustulatus* (a) and *Chilocorus kuwanae* (b).

TABLE 3

G-TEST FOR INDEPENDENCE (REF. 20) OF THE FORAGING BEHAVIOR OF ADULTS AND LARVAE OF THE PREDATORS *CHILOCORUS BIPUSTULATUS* AND *CHILOCORUS KUWANAE*

<i>Hypothesis tested</i>	<i>df</i>	<i>G</i>
Adults		
Angle x Species independence	5	32.88 **
Angle x Time independence	15	420.15 **
Species x Time independence	3	47.19 **
Angle x Species x Time interaction	15	43.77 **
Angle x Species x Time independence	38	543.99 **
Larvae		
Angle x Species independence	5	43.75 **
Angle x Time independence	15	68.74 **
Species x Time independence	3	12.88 *
Angle x Species x Time interaction	15	43.54 **
Angle x Species x Time independence	38	168.91 **

* $P < 0.01$; ** $P < 0.001$.

change, slowing down the speed of search, and increasing the number of turns (Table 2). However, following an encounter, *C. kuwanae* was faster (during the second and third 10-sec periods), and turned more frequently (only during the second period) than *C. bipustulatus*. *C. kuwanae* also reverted to its searching speed more rapidly than *C. bipustulatus* (Table 1). Moreover, *C. kuwanae* maintained this speed together with a large number of turns, thus efficiently covering a wider area during its search.

When the angle turned while searching is classified into groups (see Materials and Methods), it is found that both species distributed their turns almost evenly between left and right (Fig. 3). There was a tendency to increase the angle turned immediately following a successful encounter, and also to revert to the original behavior following the encounter. The main difference between the adults of the two species lies in their basic searching strategy. *C. bipustulatus* searched for its host with a high frequency of turns of Group 1 (Fig. 3a), whereas *C. kuwanae* searched along a much smoother path, as indicated by a high frequency of turns of Group 0 (Fig. 3b). The rate and angle of turns of the species changed significantly both within and between species (Table 3).

Larvae

The larvae of both species searched for prey using a similar number of turns per unit of time (2.7-3.0) and a similar degree of change in angle (30-34°/cm). However, *C. bipustulatus* were significantly faster (Table 2) than *C. kuwanae* (0.52 vs

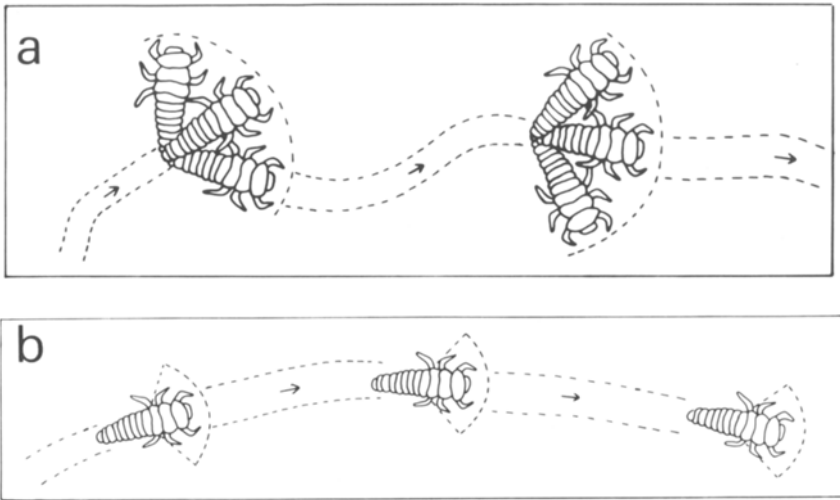


Fig. 5. Schematic representation of the arc-type movement of larvae of *Chilocorus bipustulatus* (a) and *Chilocorus kuwanae* (b) searching for prey.

0.27 cm/sec, respectively; Table 1). Moreover, following a successful encounter, *C. bipustulatus* responded more vigorously than *C. kuwanae* by significantly increasing the number and size of their turns, while *C. kuwanae* continued their pre-encounter rate of search (Table 1). Larvae of the two species were significantly slower than the adults and had a lower number of turns (Table 2). As with the adults, the turns of larvae of both species were distributed almost equally to the right and left (Fig. 4). As time elapsed following a successful encounter, the pattern of search of both species approached that prior to the encounter. The differences between and within species were significant (Table 3).

While searching for prey, the larva attached the end of its abdomen to the substrate, following which it proceeded with an arc-type movement (Fig. 5a), thus enlarging the actual area actively covered. While both species employed this tactic, *C. bipustulatus* used it more frequently than *C. kuwanae*. However, the latter species examined the immediate area on either side of its tracks with frequent narrow arc movements without actually stopping (Fig. 5b).

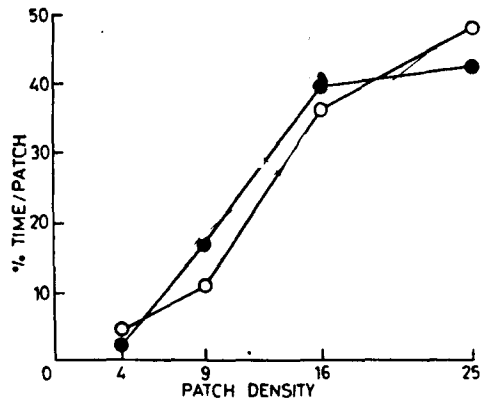


Fig. 6. Behavioral response of adults of *Chilocorus bipustulatus* (black dots) and *Chilocorus kuwanae* (circles) to increasing densities of the host.

Behavioral response to host density

Adults of both species allocated an increasing proportion of their available time to patches of prey in accordance with the number of prey within these patches (Fig. 6). No differences between species were noted in this response.

DISCUSSION

The two *Chilocorus* species demonstrated similar searching tactics for prey. They moved along relatively smooth tracks before encountering their prey, and changed their paths significantly following a successful encounter. These changes were characterized by an increasing number of wide turns and are typical of the predators and parasites studied (e.g. 3,11). This behavior, which is extremely important in predation, serves as one of the few mechanisms by which larvae and adults of the genus *Chilocorus* and most probably other coccinellid beetles increase their searching efficiency. In the absence of sensory organs capable of receiving visual or chemical cues at long or medium ranges, as are known to exist in many parasitic Hymenoptera (e.g. 24,25), these predators must rely only on the rate at which they actually cover the area by physical movement. Moreover, as *Chilocorus* prey on sessile scale insect stages, they need not adopt an ambush strategy. In fact, these beetles display behavioral responses similar to those of vertebrate predators studied, or simulated with models, by various authors (e.g. 4,5; see also review by Pyke *et al.*, 19). This type of predator is assumed "not to detect food at a distance by sight, smell, or other means..." (19). Increases in the number and angles of turns following a host encounter are considered by many authors as adaptation of the predators to feed on prey that aggregate (e.g. 7,14,15). *C. bipustulatus* and *C. kuwanae* exhibit just this type of behavior. Behavioral responses (10) demonstrated in the present study, which are so important for optimizing the foraging behavior of the predator, are a direct result of this change. The total time the predator allocates to each patch can be considered as a function of the information collected by it within the patch (25). Following a successful encounter, the predator assumes a searching pattern that increases its probability of discovering additional hosts within the patch should they exist. If none is encountered, the predator gradually resumes its pre-encounter searching pattern and within 30 sec reverts to its "between patches" type of searching mode.

The present study shows that the two species have similar types of searching strategies but differ significantly in the intensity of their responses. *C. bipustulatus* 4th instar larvae can be considered to be more efficient than *C. kuwanae* in their search for prey. Although *C. bipustulatus* larvae demonstrate a similar change in angle and mean number of turns as *C. kuwanae*, the former are significantly faster, thus covering greater areas during their search. This is the case also following successful encounter, together with the added advantage of a greater number of turns by *C. bipustulatus*.

Among the adults it is necessary to differentiate between the searching behavior "between" and "within" patches. Adult *C. bipustulatus* are more efficient "between patches" searchers, due to a more circuitous pathway (Fig. 3), and *C. kuwanae* are more efficient "within patch" searchers. They are faster and turn more frequently, thus having a greater chance of encountering additional prey in the same patch. These differences between the tactics of the two species render the quantitative estimation of their respective effectiveness problematic.

A final decision as to the more efficient biological control agent cannot be based solely on their searching attributes. Other factors, intrinsic (e.g. fecundity, rate of food consumption) as well as environmental (e.g. temperature and relative humidity), must also be considered.

ACKNOWLEDGMENT

This report was supported by Grant No. I-138-79 from the United States – Israel Binational Agricultural Research and Development Fund (BARD).

REFERENCES

1. Banks, C.J. (1954) The searching behaviour of coccinellid larvae. *Anim. Behav.* 2:37-38.
2. Banks, C.J. (1957) The behaviour of individual coccinellid larvae on plants. *Anim. Behav.* 5:12-24.
3. Carter, M.C. and Dixon, A.F.G. (1982) Habitat quality and foraging behaviour of coccinellid larvae. *J. Anim. Ecol.* 51:865-878.
4. Cody, M.L. (1971) Finch flocks in the Mohave desert. *Theor. Popul. Biol.* 2:142-158.
5. Cody, M.L. (1974) Optimization in ecology. *Science, N. Y.* 183:1156-1164.
6. Cook, R.M. and Hubbard, S.F. (1977) Adaptive searching strategies in insect parasites. *J. Anim. Ecol.* 46:115-125.
7. Dixon, A.F.G. (1959) An experimental study of the searching behaviour of the predatory coccinellid beetle *Adalia decempunctata* (L.). *J. Anim. Ecol.* 28:259-281.
8. Fleschner, C.A. (1950) Studies on searching capacity of the larvae of three predators of the citrus red mite. *Hilgardia* 20:233-265.
9. Formanowicz, D.R. Jr. (1982) Foraging tactics of larvae of *Dytiscus verticalis* (Coleoptera: Dytiscidae): The assessment of prey density. *J. Anim. Ecol.* 51:757-767.
10. Hassell, M.P. (1966) Evaluation of parasite or predator responses. *J. Anim. Ecol.* 42:693-736.
11. Hassell, M.P. and Southwood, T.R.E. (1978) Foraging strategies of insects. *A. Rev. Ecol. Syst.* 9:75-98.
12. Hubbard, S.F. and Cook, R.M. (1978) Optimal foraging by parasitoid wasps. *J. Anim. Ecol.* 47:593-604.
13. Kamburov, S.S., Nadel, D.J. and Kenneth, R. (1967) Observations on *Hesperomyces virescens* Thaxter, a fungus associated with premature mortality of *Chilocorus bipustulatus* L. *Israel J. agric. Res.* 17:131-136.
14. Laing, J. (1938) Host finding by insect parasites. II. The chance of *Trichogramma evanescens* finding its hosts. *J. exp. Biol.* 15:281-302.
15. Mitchell, B. (1963) Ecology of two carabid beetles, *Bembidion lampros* (Herbst) and *Trechus quadristriatus* (Schrank). I. Life cycles and feeding behaviour. *J. Anim. Ecol.* 32:289-299.

16. Murdie, G. and Hassell, M.P. (1978) Food distribution, searching success and predator-prey models. *in*: Hiorns, R.E. [Ed.] *The Mathematical Theory of the Dynamics of Biological Populations*. pp. 87-101. Academic Press, London.
17. Nadel, D.J. and Biron, S. (1964) Laboratory studies and controlled mass rearing of *Chilocorus bipustulatus* L., a citrus scale predator in Israel. *Riv. Parassit.* **25**:195-206.
18. Podoler, H. and Henen, J. (1983) The effects of constant temperatures on developmental time and survival of two coccinellid beetles of the genus *Chilocorus*: A comparative study. *Phytoparasitica* **11**:167-176.
19. Pyke, G.H., Pulliam, H.R. and Charnov, E.L. (1977) Optimal foraging, a selective review of theory and tests. *Q. Rev. Biol.* **52**:137-154.
20. Sokal, R.R. and Rohlf, E.J. (1969) *Biometry*. W.H. Freeman & Company, San Francisco, CA.
21. Stamp, N.E. (1982) Searching behaviour of parasitoids for web-making caterpillars: A test of optimal searching theory. *J. Anim. Ecol.* **51**:387-395.
22. Storch, R.H. (1976) Prey detection by 4th stage *Coccinella transversoguttata* (Coleoptera: Coccinellidae). *Anim. Behav.* **24**:690-693.
23. Stubbs, M. (1980) Another look at prey detection by coccinellids. *Ecol. Ent.* **5**:179-182.
24. Waage, J.K. (1978) Arrestment responses of the parasitoid *Nemeritis canescens* to contact chemical products by its host, *Plodia interpunctella*. *Physiol. Ent.* **3**:135-146.
25. Waage, J.K. (1979) Foraging for patchily-distributed hosts by the parasitoid, *Nemeritis canescens*. *J. Anim. Ecol.* **48**:353-371.