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Exploration of Wheat Leaves by *Coccinella septempunctata* L. (Coleoptera, Coccinellidae) Larvae

A. Ferran[1] and M. Deconchat[1]

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A new method for the quantification of insect movements on leaves is presented and applied to larvae of a wheat aphid predator, C. septempunctata. *The method results from behavioral definition of positions adopted by this predator during its advance along the wheat leaf. Through a factor analysis of multiple correspondences, the method allowed specification of some aspects of predator movements on plants, especially the frequency of position associations, to give a new definition of local search and to describe some behavioral interactions with aphids. The consequences for predator efficiency are discussed.*

KEY WORDS: *Coccinella septempunctata;* position; search pattern; predator-prey relationships; predator efficiency.

INTRODUCTION

When predators leave one prey patch for another, their paths are roughly linear and their walking speed is high [*ranging* (Dusenbery, 1989)]. After feeding on a prey in a patch, they follow sinuous paths and their speed is slower [*local search* (Bell, 1990)]. This search tactic and fan-shaped movements of the body [*casting* (Curio, 1976)] provide accurate scanning of the area surrounding the capture point.

Ranging and local search, which have been described for artificial, smooth surfaces, probably undergo modifications under natural conditions. Among biotic factors, plants, through their physical (Carter *et al.*, 1984), and perhaps chemical

[1]Station de Zoologie et de Lutte biologique, 37, boulevard du Cap, 06600 Antibes, France.

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(Obata, 1986), features, guide predators and force them to exhibit special search tactics especially given their need to cling on to the substrate. Therefore, predator efficiency depends on the positions that they adopt to explore plants as well as on density, distribution and defensive reactions of prey (Hajek and Dahlsten, 1987, Wratten, 1976).

We report here a study on movement and spatial relationships with prey of the last larval instar of *Coccinella septempunctata* L. searching on wheat leaves for *Sitobion avenae* (Hom., Aphididae).

MATERIALS AND METHODS

Individued larvae were released one by one on a wheat leaf blade near the stem and filmed as soon as they appeared in the field of a camera focused on an aphid colony.

Coccinellid larvae were obtained from a laboratory stock fed on the aphid, *Acyrtosiphon pisum* Harris. Before being used, larvae were starved for 12 h and kept at 22°C and 70 to 80% relative humidity during this period as well as during the experiment. Five days before the experiment, potted wheat plants with five leaves were infested with a laboratory strain of *Sitobion avenae*. For the experiments, plants with a colony of 19 ($\pm$2) naturally distributed aphids were selected.

The video setup consisted of a camera with a 35 to 200-mm telephoto lens, a tape recorder, and a TV monitor. The camera's field was 5.6 $\pm$ 0.3 cm^2.

During exploration of wheat leaf blades, coccinellid larvae follow the leaf edge (Mark, 1977). Using observations, we classified four positions called sagittal, parallel, angular, and overlapping (Fig. 1). We added an artificial position, off-camera (OC). It corresponds to positions without a precise duration which were recorded when the coccinellid larvae walked into or out of the camera field. All positions may occur either on the upper side of the leaf, where aphids normally reside (P), or on the opposite side (V).

For these positions, various events were scored: unsuccessful encounters with prey (CT), prey captures (PC), drumming with forelegs on the leaf (DR), and lateral movements of the head (HM).

To define the main behavioral features of the positions and to specify their temporal relationships, a "time-description" matrix was built. For every position adopted by each coccinellid larva (total number, 33) while within the field of the camera, the following descriptive variables were scored.

(1) The position at time *t* and its orientation toward or away from aphids (P or V).
(2) The presence and the nature of the most frequent event during this position.

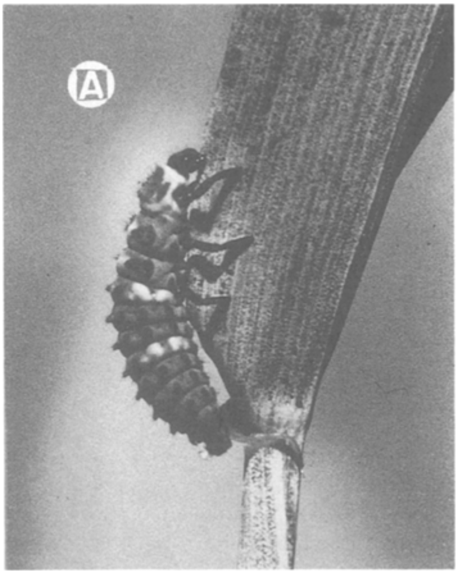


Fig. 1. The four positions adopted by last-instar larvae of *C. septempunctata* on wheat leaves: sagittal (A), parallel (B), angular (C), and overlapping (D) positions.

(3) The speed of movement. The duration of the position was measured by means of the clock on the tape recorder (accuracy, ± 1 s); the corresponding distance traveled, with an imposed graduated ruler (mm).
(4) The nature of the previous position and its orientation relative to aphids (P or V).

The values for each variable are shown in Table I.

The resulting data, where every record (every position at time*t*) was considered as an observation, was submitted to factor analysis and then to a hierarchical classification. The use of 0.15 as a cutoff level on the graphical representation of this hierarchy separated seven homogeneous groups characterized by the frequency of the different variables.

For prey colonies, the number of aphids dropping off the leaf and the

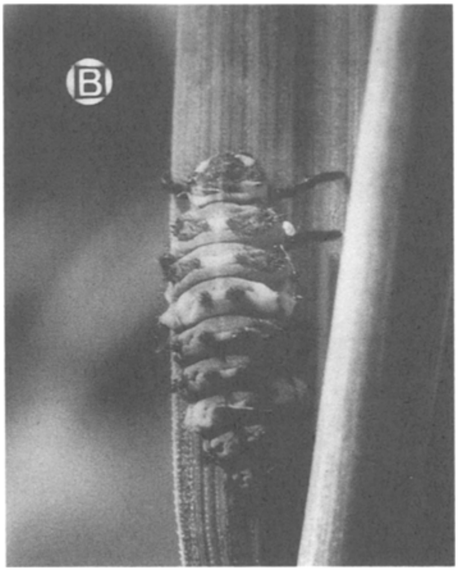


Fig. 1. Continued

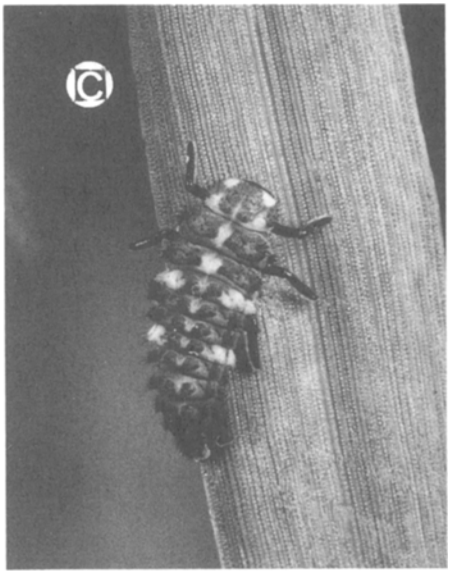
number of aphids escaping but remaining on the leaf were scored before and after the first capture.

RESULTS

Behavioral Definition of Positions and Their Temporal Relationships

The "Time–description" matrix, by separating seven groups, increased the number of positions over those originally proposed (Fig. 2).

Group 1 (G1) was made up mostly of the sagittal position (80.0%; Fig. 2A), which followed the off-camera position (67.7%) and, more seldom (19.4%), the overlapping position (Fig. 2B). This group was characterized by scarceness of prey contacts and captures (Fig. 2C), slower movements (Fig. 2D), and long



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durations. The larvae often adopted this position to eat prey caught in another position.

This analysis distinguished an another group (G6) dominated by the sagittal position (93.3%). Group 6 followed mainly the overlapping position (54.0%) and differed from group 1 by more contacts and drumming, faster speed, and intermediate duration.

Group 2 was characterized mainly by the overlapping position (69%; Fig. 2A), coming after the sagittal position (62.0%; Fig. 2B). It applied to slow larvae which caught many aphids (71.7%).

The overlapping position also predominated in group 5 (92.0%; Fig. 2A). Group 5 differed from Group 2 by far fewer prey captures, many more prey contacts, and more casting (Fig. 2C) and by faster mobility (Fig. 2D). At times, the larva's body might not be strictly perpendicular to the leaf edge. This inferred position should allow moving and prospecting simultaneously. In the field, this

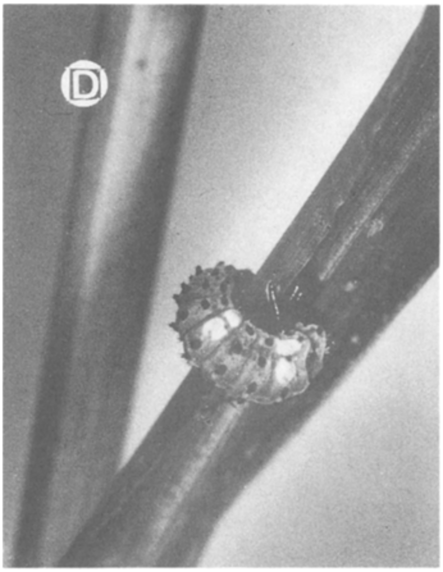


Fig. 1. Continued

position might be exhibited by larvae walking down a wheat stem or a vertical leaf.

Group 3 contained all the positions on the side (V) of the leaf without aphids. These positions mainly followed the sagittal position (56.0%, Fig. 2B). The origin of this group was artificial since the corresponding events and movements could not be recorded.

In Group 4, the parallel (58.3%) and sagittal (25.0%) positions predominated (Fig. 2A). They followed the angular position (50.8%; Fig. 2B). In this group, fast larvae often contacted aphids, but prey captures were infrequent (Fig. 2C).

Group 7 was simultaneously characterized by angular (50.0%) and sagittal (36.0%) positions (Fig. 2A), which followed the parallel position (53.6%; Fig.

Table I. Variables and Values Used to Build the "Time–Description" Matrix

Variable	Value	Definition
Position at time *t*, toward aphids (P) or not (V).	Sagittal	
	Parallel	
	Angular	
	overlapping	
Previous position, toward aphids (P) or not (V).	All previous positions	
	Off camera	
Events during position at time *t*	None	No events
	CT	Contact with prey
	PC	Prey-catching
	DR	Drumming
	HM	Casting
Larval speed during position at time *t*	Null	none measured
	Low	<0.1 cm/s
	Strong	>0.1 cm/s

2B). For this group, mobile larvae frequently contacted aphids, but prey captures were rare (Fig. 2C).

Some features of the temporal organization of coccinellid movement along wheat leaves may be deduced from these results. Larvae arriving on the leaf edge or eating an aphid remain in the sagittal position, which seems to be the hinge for the others. Then they adopt the overlapping position and later come back to the sagittal one (Fig. 2, Table II): temporal relationships between these two positions are the strongest. There are similar, though less frequent, reciprocal exchanges between the angular and the parallel positions. Conversely, the relationships between overlapping and angular positions are virtually absent when the larvae remain on the same side of the leaf.

In predators, local search appears after they have eaten a single prey. The comparable duration and frequency for each position between feeding (n: 25) and nonfeeding (n:8) larvae give another meaning to this search tactic. Prey-catching larvae remained longer in the camera field (Table III), their immobility resulting from feeding. In prey-catching coccinellids, the sagittal position was more scarce, whereas the angular and overlapping positions were less scarce. In these two positions, particularly in the overlapping one (Fig. 2), mobility is low, and prey-catching (Group 2), unsuccessful contacts, drumming, and casting (Group 5) are more numerous. In the overlapping position the explored area measured by the mean distance between the larval head and the edge of the leaf (0.26 $\pm$ 0.07 cm, 95% confidence interval) is equal (angular position, 0.30 $\pm$ 0.06 cm) or superior to those scored in the other positions (sagittal position, 0.11 $\pm$ 0.02 cm; parallel position, 0.15 $\pm$ 0.06 cm).

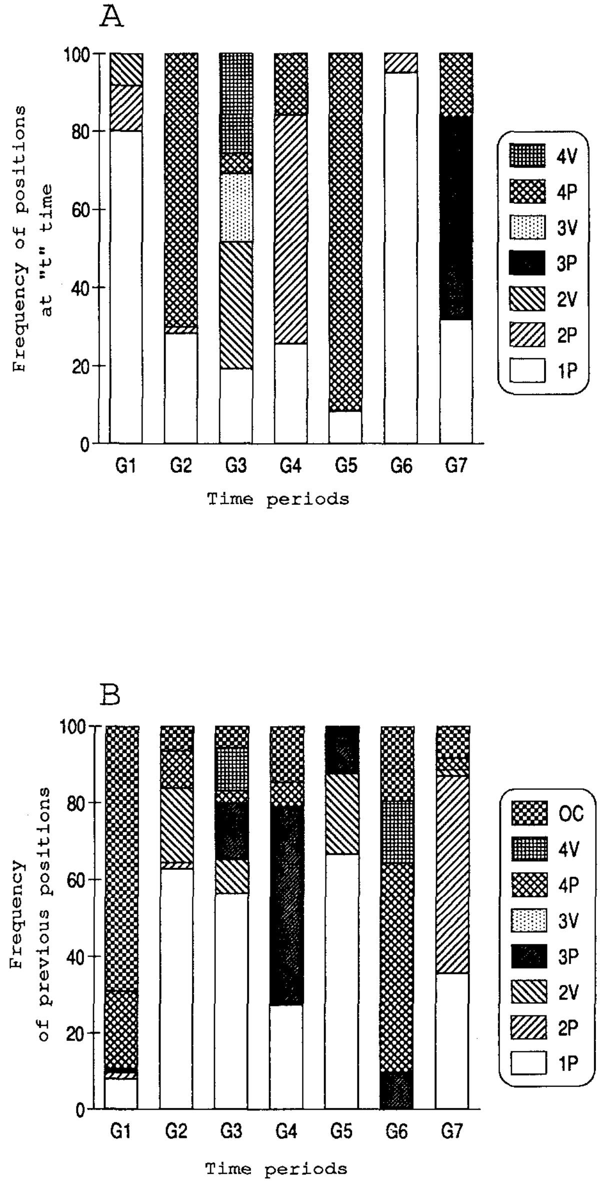
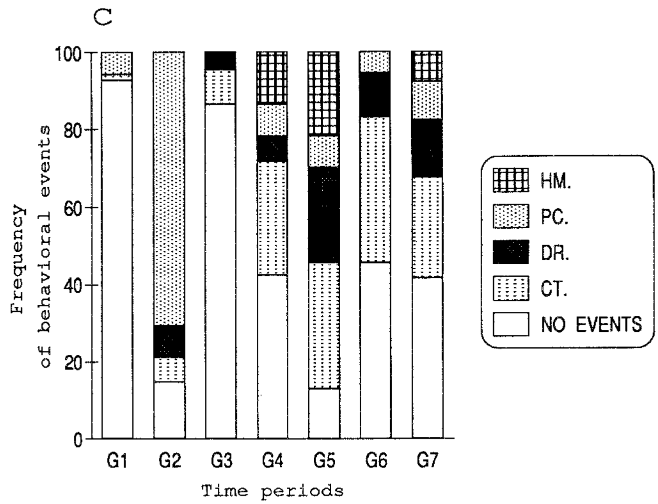


Fig. 2. Definition of positions according to previous position, percentage of behavioral events, and speed classes (D). Positions: 1, sagittal; 2, parallel; 3, angular; 4, overlapping, OC, off-camera; P, orientation toward the leaf side with aphids; V, orientation toward the leaf side without aphids. Events: contact with prey (CT); drumming (DR); prey capture (PC); casting (HM). Speed classes: see Table I.



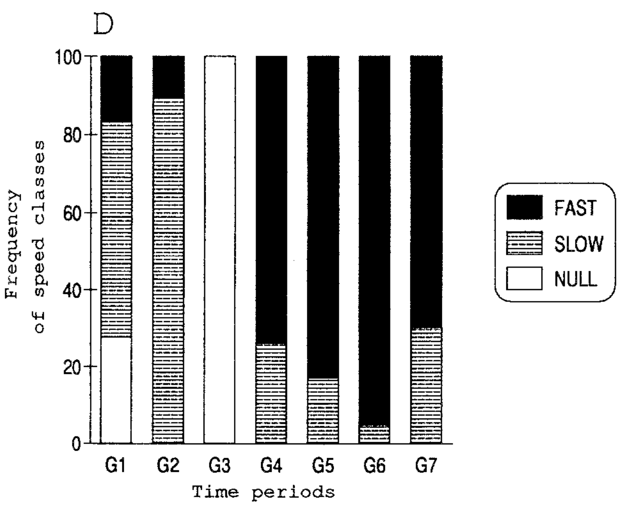


Fig. 2. Continued

Table II. The association in Pairs of the Different Positions: For All Larvae, Number of Times (Frequency) Where Every Position (Vertically) Is Followed by One of the Three Others (Horizontally) – Total Number of Pairs (389)

Following position	Previous position			
	Sagittal	Parallel	Angular	Overlapping
Sagittal	—	26.0	41.7	80.2
Parallel	16.2	—	37.6	17.6
Angular	32.4	48.1	—	2.2
Overlapping	51.4	25.9	15.3	—

Table III. Influence of Prey-Catching on Prey-Search Behavior of Coccinellids on the Wheat Leaves

Parameter	Larvae		Test
	Without prey-catching	With prey-catching	(t)
Time spent in the field (D)	25.6(11.7)[a]	242.8(53.6)	8.2*
Position duration			
(% of D)			
Sagittal	69.4(15.7)	51.8(16.1)	2.7*
Parallel	19.4(13.4)	27.2(12.6)	1.5
Angular	3.1 (2.9)	6.4 (3.3)	2.7*
Overlapping	8.1 (9.9)	29.6 (8.7)	4.8*
Position frequency			
(% of the total number)			
Sagittal	57.3(17.8)	40.0 (5.5)	2.7*
Parallel	20.7(12.3)	24.1 (7.7)	0.7
Angular	8.1 (4.9)	16.2 (5.5)	4.0*
Overlapping	12.9 (8.4)	19.7 (5.2)	3.2*
Time spent (% of D) in			
Sagittal	52.4(15.0)	33.2(13.0)	2.1
(P) positions	7.5 (5.3)	57.4(13.4)	7.2*
(V) positions	40.1(10.3)	9.3 (5.7)	5.9*
Position frequency			
(% of the total number)			
Sagittal	37.6(11.9)	27.2 (4.2)	1.9
(P) positions	14.3 (8.6)	53.5 (6.1)	8.2*
(V) positions	48.1(12.4)	20.1 (5.7)	4.6*

[a]Confidence interval at $p < 0.05$.
*Significant difference.

Prey-catching larvae explored specifically the upper leaf side (P), where the experimental aphid colony was located (Table III). In contrast, nonfeeding coccinellids tended to be more often on the lower side (V) of the leaf.

Influence of Prey Capture on Aphid Behavior

Among all the observations of larvae, only two aphids were walking in the 10 s prior to the first prey-catching. In the 10 s following capture, 25% of the aphids in a colony were on the move. They did not react to coccinellid's approach, although some contacts induced aphids to drop from the leaf. Once caught, the captured aphid very quickly broke up the colony, probably by the emission of alarm pheromones (Dawson *et al.*, 1987). The aphids located near a feeding predator walked away first, and then the movement spread to the whole colony. In a colony containing roughly 20 aphids, the following results were obtained: captures, 9%; walking away, 35%; falls; 12%; and remainder, 44%.

DISCUSSION

In Coccinellids, prey perception occurs only at short range (Nakamuta, 1984, 1985; Storch, 1976; Stubb, 1980). The plant, through its physical features, guides predator movement and compels predators to adopt particular tactics of leaf exploration. Like prey density and distribution, plant morphology affects predatory efficiency.

The last-instar larvae of *C. septempunctata* walk along the wheat leaf edge, which they clutch with their legs and/or their anal pseudopod. For moving and prospecting the leaf blade, predators present four elementary positions, i.e., sagittal, parallel, angular, and overlapping. But a more behavioral definition of these positions allows one to distinguish six positions, particularly new overlapping and sagittal positions. All these positions present preferential correlations over time, e.g., the temporal association between the overlapping and the sagittal positions or between the angular and the parallel positions, which suggest an organization of movement during wheat leaf exploration.

On an artificial plane surface, the larvae present two moving tactics, ranging and local search, which differ from one another in orientation stimuli, path sinuosity, and speed. Characterization of these tactics is more difficult on plants. The sagittal position, giving its low capture rate, high speed, and relationships with most other positions, may be considered as ranging. Local search adopted by larvae after feeding should be associated with greater importance of positions for leaf exploration, particularly with the overlapping position, and with preferential localization on the leaf side where the aphid colony occurs. Nonfeeding coccinellid larvae tended to be more often on the lower leaf side, which is usual among these predators (Dixon, 1959). This difference in location may be explained by preferential exploration of the leaf side after capture of the first aphid.

During leaf exploration, contacts occurred during each position without significant differences. The frequency of contacts depended on aphid distribution, which was rather variable in this experiment. Captures, drumming, and casting were higher in the overlapping position.

Even in the case of angular and overlapping positions, a region on each side of the leaf vein is not explored and aphids staying there are not captured. The width of this area probably depends on the predator (species, stage), the plant (leaf size, roughness, hairiness), and the aphids (localization, number). In wheat crops (Ferran *et al.*, 1989), a significant proportion of the aphid population is located near the vein: *Metopolophium dirhodum* Walk., 59.9%; *Rhopalosiphum padi* L., 21.6%; and *Sitobion avenae*, 43.6%. This unprospected area may be considered as evidence of a poor predator efficiency in this coccinellid or as an example of resource partitioning among aphidophagous insects (Coccinellidae, Syrphidae, Chrysopidae) in the wheat biocenosis.

Coccinellids disturb aphid colonies. They induced falling of aphids from the plant, often by direct contact and movements which probably resulted from the production of alarm pheromones by the first aphid caught. Coccinellid larvae are able to catch mobile prey during successive explorations of the same plant. In a wheat field in early spring, the daily diet of coccinellids contains approximately 30.0% aphids walking on the ground (Ferran *et al.*, 1991). Thus, drumming with the forelegs on the leaf is perhaps intended to alarm the aphids and so to cause them to walk on the leaf or to fall from the plant.

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