Sources of Variability in the Transition from Extensive to Intensive Search in Coccinellid Predators (Homoptera: Coccinellidae)

A. Ferran,[1] **M. Ettifouri,**[1] **P. Clement,**[2] **and William J. Bell**[3]

In an environment structured by habitats, prey patches, and prey, predators such as coccinellids have two movement modes. The extensive search and the intensive search which results from prey capture are adopted for patch localization and exploration, respectively. The variability of changes from extensive search to intensive search was studied in larvae of the aphidophagous coccinellid Semiadalia undecimpunctata *to find out their possibility of adaptation to a fluctuating environment. The temporal organization of coccinellid movements appears far more complicated than the generally accepted succession of extensive search, feeding, and intensive search. Their paths are characterized by the presence of time intervals devoted to intensive search before feeding, a highly variable path response after prey consumption (larvae may adopt intensive search immediately, later, or never), and the alternation of time periods devoted to either extensive search or intensive search after prey ingestion. This interindividual variability suggests that coccinellids have the ability to adapt to heterogeneity or short-term changes in environmental conditions, particularly in prey distribution. These results are in favor of the use of these predators in biological control programs.*

[1] Laboratory of Invertebrate Biology, 37 Bd. du Cap, 06600 Antibes, France.
[2] Laboratory of Ethology, Claude Bernard University, 43 Bd. du 11 novembre 1918, 69622 Villeurbanne, France.
[3] Department of Entomology, University of Kansas, Lawrence, Kansas 66045.

INTRODUCTION

Predators live in a complex and changing environment, particularly where the quality, the density, and the spatiotemporal distribution of preys are concerned. In response to these environmental changes, predators can modify their feeding preferences and (or) their prey searching behavior, thus improving their foraging efficiency (Drost *et al.*, 1988). Nevertheless, due to the variability of the searching behavior in predator populations (Bell, 1991), many individuals are probably able to forage efficiently in this fluctuating environment without learning how. The knowledge of the range of this variability is important for biological control because predators are often released in environmental conditions (climate, plant, prey) that are unusual for them. There are few examples of learning in coccinellids and they concern mainly change in prey preferences (Murdoch and Marks, 1973; Houck, 1986). The interindividual variability of their searching behavior is still unknown.

Coccinellids exhibit two types of walking pattern during search for prey (Nakamuta, 1985). Extensive search (Bond, 1980) functions in the search for patches and is characterized by long linear paths and a fast speed. Intensive search (Bond, 1980) for path exploration results from two mechanisms: fan-shaped movements of the body (Curio, 1976) and a lowering of the linear speed and an increase in the number of stops and angular speed. In predators, intensive search appears after a prey capture and, for this reason, has been called "success-motivated search" (Vinson, 1977). Without new captures, extensive search progressively replaces intensive search. The subsequent linear movements reduce the probability of encounters with new prey and thereby favor leaving the explored patch (Bell, 1990).

The interindividual variability of the transition from extensive search to intensive search was studied in a laboratory larval population of the aphidophagous coccinellid *Semiadalia undecimpunctata* Schn. This work is based on the assumption of Delcomyn and Cocatre-Zilgen (1988) that the differences between path parameters before and after prey capture may lead to particular motor patterns of extensive and intensive search.

MATERIALS AND METHODS

The coccinellid and its prey *Acyrthosiphon pisum* Harris (Hom., *Aphidae*) were reared continuously in the laboratory.

Fourth-instar larvae of this stock (20 to 25 mg) were isolated in 2 × 3-cm plastic vials. They were each fed five aphids weighing from 1.00 to 1.25 mg. Four hours later, coccinellids that had eaten at least three aphids were starved for 12 h before each experiment. This procedure was used to equalize their trophic state (Nakamuta, 1985).

Each larvae (*n*: 62) was filmed for 80 s, then fed one aphid. At the end of

feeding, it was filmed again for 6 min. Larvae were filmed in a white arena (height, 40 cm; diameter, 50 cm). The experiment was done at 22°C · 1°C and 70 to 80% relative humidity, under a 16 L:8 D light cycle.

A video tape recorder and a computer equipped with a French card (SECAD Public Company) for video picture analysis and specific software (Clément, 1983; Clément and Luciani, 1985; Coulon and Charras, 1983; Luciani and Chassé, 1983) were used to calculate automatically in real time the coordinates of the center of gravity every 0.04 s (25 frames/s) and, from these, derive the path parameters. For coordinate computation, the screen of the filmed area included the same number (512) of lines and columns, the paths were automatically smoothed (average of five successive points), and all coordinate pairs (25/s) were recorded.

The paths were divided into lengths of 20 s, thus 4 and 24 path lengths, respectively, before and after feeding. Each path length was characterized by (a) number of stops (the rapid variation in this parameter after feeding was responsible for our choice of the path length duration), (b) total distance moved (mm), (c) linear speed (mm/s; excluding stop duration), and (d) angular speed (deg/s); computed from successive positions of the center of gravity of the ladybird body and taking into account only the direction changes. The fan-shaped movement of the body (casting) occurred only when coccinellids had stopped (Banks, 1957).

The data, arranged in a table where rows corresponded to successive path lengths and columns to previous path parameters, were subjected to various statistical analyses (a) to describe the variations of path parameters before and after feeding, (b) to calculate variability between time periods and individuals (these comparisons were made with the F test), and (c) to analyze the underlying causes of variability.

All path lengths characterized by the four previous parameters (without statistical transformation) were subjected to a principal components analysis (Benzecri, 1979) and a hierarchical classification (Ward, 1963). By sectioning the graphic representation of this hierarchy at various levels, the successive path lengths of all larvae were classified into groups (i.e., movement patterns characterized by different averages for each parameter). This classification made it possible to study the variation of group frequency in the successive 20-s periods before and after prey consumption for the larval population and to specify the temporal organization of individual movements.

RESULTS

Variability of Path Parameters

Before feeding (path lengths 1 to 4), the path parameters were not significantly different (Tables Ia and b). Prey consumption induced a significant change of path parameter values in the fifth path length: an increase in stop number, angular speed, a decrease in the distance traveled, and linear speed (Table Ia).

Table Ia. Comparison of Path Parameters Before (Path Lengths 1 to 4) and After (Path Length 5) Prey Consumption

Path parameter	Successive path length				
	1	2	3	4	5
Number of stops (in 20 s)	29.9 ± 6.5	34.3 ± 7.8	33.4 ± 7.6	29.3 ± 6.4	70.0 ± 8.6
Traveled distance (mm)	164.4 ± 16.8	163.4 ± 17.4	157.0 ± 17.2	192.9 ± 17.7	87.4 ± 12.9
Linear speed (mm/s)	10.1 ± 0.7	9.9 ± 0.7	9.4 ± 0.7	9.8 ± 0.7	7.7 ± 0.5
Angular speed (deg/s)	24.5 ± 3.5	26.5 ± 4.7	24.7 ± 4.0	22.7 ± 3.1	55.9 ± 7.8

Table Ib. Variability in Path Parameters Between Tests and Among Individuals Before and After Feeding

Path parameter	Comparison		
	Between tests		Among individual larvae
	1 vs 4	1 to 5	
Number of stops	0.5 ns	20.2*	7.7*
Traveled distance	0.1 ns	18.7*	10.5*
Linear speed	0.8 ns	8.8*	15.3*
Angular speed	0.6 ns	26.7*	7.5*

*F value, $P < 0.001$.

The differences in each path parameter from the first to the fifth path length were shown by separating each path parameter into equal classes then calculating the frequency of path lengths falling into each class. Thus, for example, "number of stops" was divided into the four classes, 0–34, 35–70, 71–105, and 106–142 stops (Fig. 1). During the first four periods, some of the path parameter values corresponded more closely to intensive search than to extensive search. This was apparently due to larvae variability among individual larvae. This interindividual variability is clearly demonstrated in Tables Ia and b, where all of these comparisons are significantly different.

Comparing larvae immediately after feeding (path length 5) and 5 min later (path length 24), significant differences were found in all parameters. The variability among larvae was also significant (Tables IIa and b).
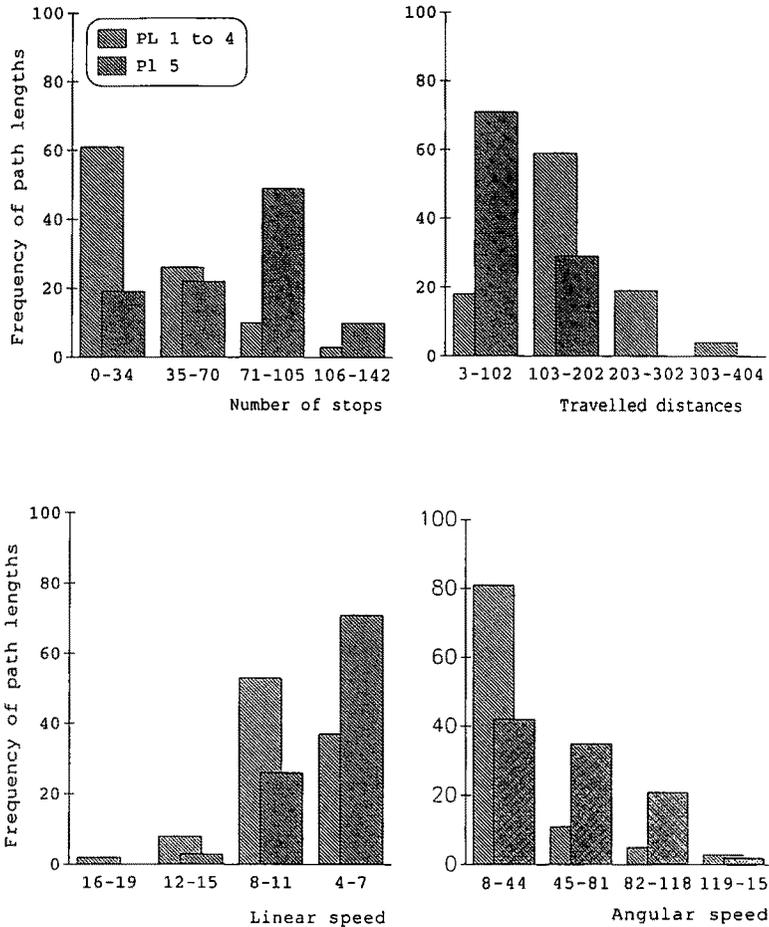
Fig. 1. Changes in path parameters from prefeeding (path lengths 1 to 4) to immediately after feeding (path length 5).

Reasons for Path Parameter Variability

In the principal-component analysis, the first two main axes explained 90.2% of the total inertia. The four parameters were linked in pairs, the number of stops with angular speed and the linear speed with traveled distance. The hierarchical classification led to the path length distribution represented in Fig. 2. Classes are represented on the OX axis by thick lines whose length is proportional to their respective path length number. As path length classes become statistically more closely related, the more the vertical thin lines linking them are close to zero on the OY axis (aggregation index). The vertical dashed lines

Table IIa. Comparison of Path Parameters After Prey Consumption (Path Lengths 5 to 24.)

Successive path lengths	Number of stops (in 20 s)	Distance traveled (mm)	Linear speed (mm/s)	Angular speed (deg/s)
5	70.0 ± 8.6	87.4 ± 12.9	7.7 ± 0.5	55.9 ± 7.8
6	57.9 ± 9.9	115.4 ± 15.3	8.3 ± 0.7	43.2 ± 7.9
7	56.7 ± 9.4	111.8 ± 15.8	8.2 ± 0.6	43.7 ± 8.1
8	55.3 ± 9.4	116.6 ± 15.6	8.5 ± 0.7	40.7 ± 7.4
9	50.3 ± 9.6	119.7 ± 17.4	8.7 ± 0.8	41.1 ± 8.6
10	52.1 ± 9.5	114.9 ± 19.2	8.4 ± 0.7	44.3 ± 8.8
11	51.4 ± 10.4	117.6 ± 21.3	8.6 ± 0.8	46.1 ± 13.9
12	45.9 ± 10.2	119.9 ± 21.3	8.9 ± 0.9	39.3 ± 9.4
13	50.2 ± 10.6	123.4 ± 21.7	8.8 ± 0.9	39.5 ± 9.6
14	47.9 ± 10.8	112.3 ± 20.2	8.6 ± 0.9	40.8± 10.0
15	48.0 ± 12.0	109.5 ± 18.6	8.8 ± 0.8	40.0 ± 9.5
16	52.0 ± 10.8	104.6 ± 22.1	10.1 ± 0.9	46.4 ± 8.7
17	50.6 ± 11.0	108.0 ± 19.6	09.5 ± 1.0	41.9 ± 7.2
18	36.8 ± 12.7	153.6 ± 23.0	11.3 ± 1.1	32.6 ± 7.2
19	44.6 ± 9.8	110.2 ± 17.3	10.2 ± 1.0	37.5 ± 7.3
20	32.9 ± 10.1	147.6 ± 19.6	12.2 ± 1.3	24.9 ± 10.3
21	39.2 ± 9.8	147.3 ± 19.4	11.8 ± 1.2	31.9 ± 9.9
22	31.9 ± 8.8	146.5 ± 18.2	11.3 ± 0.8	24.2 ± 10.1
23	34.1 ± 10.1	150.0 ± 20.7	11.5 ± 0.9	27.7 ± 9.9
24	33.4 ± 9.6	167.2 ± 19.9	12.2 ± 1.2	29.1 ± 10.4

Table IIb. Variability in Path Parameters Between Tests and Among
Individuals Immediately and After 400 s

	Comparison	
Path parameter	Between tests (5 vs 24)	Among individual larvae
Number of stops (in 20 s)	7.7*	26.9*
Traveled distance (mm)	3.8*	23.9*
Linear speed (mm/s)	4.1*	37.0*
Angular speed (deg/s)	6.3*	27.0*

*F value, $P < 0.001$.

defined the different path length groups. The more the section level is close to 0 (OY axis), the more these groups are statistically related.

This graph could be sectioned at at least two levels, for example, at the 0.5 and 0.08 levels. The first section (Fig. 2) isolated two groups of path lengths, the usual dichotomy of insect movements. Group 1 (GR1) corresponds to extensive search (number of stops and angular speed were lower, traveled distance and linear speed greater as in Table III). For opposite reasons, group 2 (GR2)
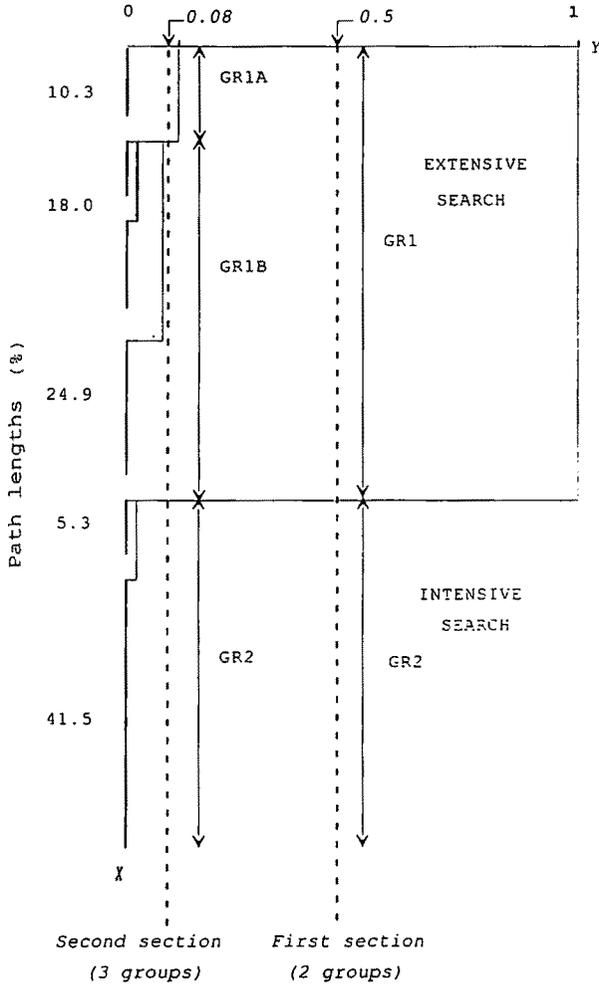
Fig. 2. Hierarchical classification of pre- and postfeeding path length: definition of movement modes and motor patterns.

represents intensive search. The second section in the graph (0.08) created a further group of path lengths (GR1B) that came from group 1 (extensive search) of the first section (Fig. 2). This intermediate extensive search included 42.9% of path lengths.

Figure 3A represents the temporal change in the frequency of groups defined by the first section (extensive, intensive search). Before feeding, the percentage of path lengths associated with extensive search is higher compared to the other group. However, 19 to 23% of them are devoted to intensive search. Despite

Table III. Grouping of Path Lengths According to a Hierarchical Classification: Characterization
of These Groups by the Corresponding Values of the Path Parameters

Path length group	Number of stops (in 20 s)	Distance traveled (mm)	Linear speed (mm/s)	Angular speed (deg/s)
GR1	37.4 ± 1.9	144.4 ± 3.1	9.6 ± 0.2	26.7 ± 1.0
GR2	91.7 ± 3.2	45.2 ± 45.2	6.1 ± 0.7	90.1 ± 2.7

Section of Fig. 2 at the level 0.5

% of path lengths: GR1, 53.2: GR2, 46.8

GR1A	16.9 ± 1.1	183.1 ± 2.7	11.1 ± 0.1	16.8 ± 0.3
GR1B	61.0 ± 2.2	101.7 ± 3.8	8.8 ± 0.2	37.2 ± 1.2
GR2	91.2 ± 3.2	45.8 ± 2.8	6.9 ± 0.1	89.9 ± 2.7

Section of Fig. 2 at the level 0.08

% of path lengths: GR1A, 10.3: GR1B, 32.9: GR2, 46.8

prior equalization of larval hunger, 41.9% of larvae had one, and sometimes two to four, path length(s) of intensive search before prey consumption.

After prey consumption both of the movement modes occurred. Intensive search was generally less frequent than extensive search except for the fifth path length, and then it progressively decreased. The presence of intensive search for up to the 28th path length depended on the time elapsed between the end of feeding and the initiation of intensive search by larvae and on the alternation of time periods devoted to either intensive or extensive search.

The larval population may be divided into three groups according to the rapidity of their motor response to prey feeding. The first group included larvae (72.6% of their total number) that adopted intensive search as soon as feeding had ceased (in the fifth path length). The second group (16%) included larvae characterized by a belated response. Intensive search appeared for up to 180 s (in the 14th path length) after prey consumption. In the third group (11.3%), intensive search was not observed at all after prey consumption. Figure 4 shows the variation of path parameters in these larval populations. The path parameters of the larvae without motor response (black points) were easily distinguishable from the others. In larvae with immediate (thick line) and belated (white points) responses, the path parameters, particularly the number of stops and the angular speed, changed for the first path length just after consumption.

After prey consumption, movements of larvae with immediate and belated response were characterized by a succession of periods devoted to either extensive search or intensive search. Most postfeeding periods (73.3%) devoted to intensive search included one to three path lengths, but some periods (10.5%)
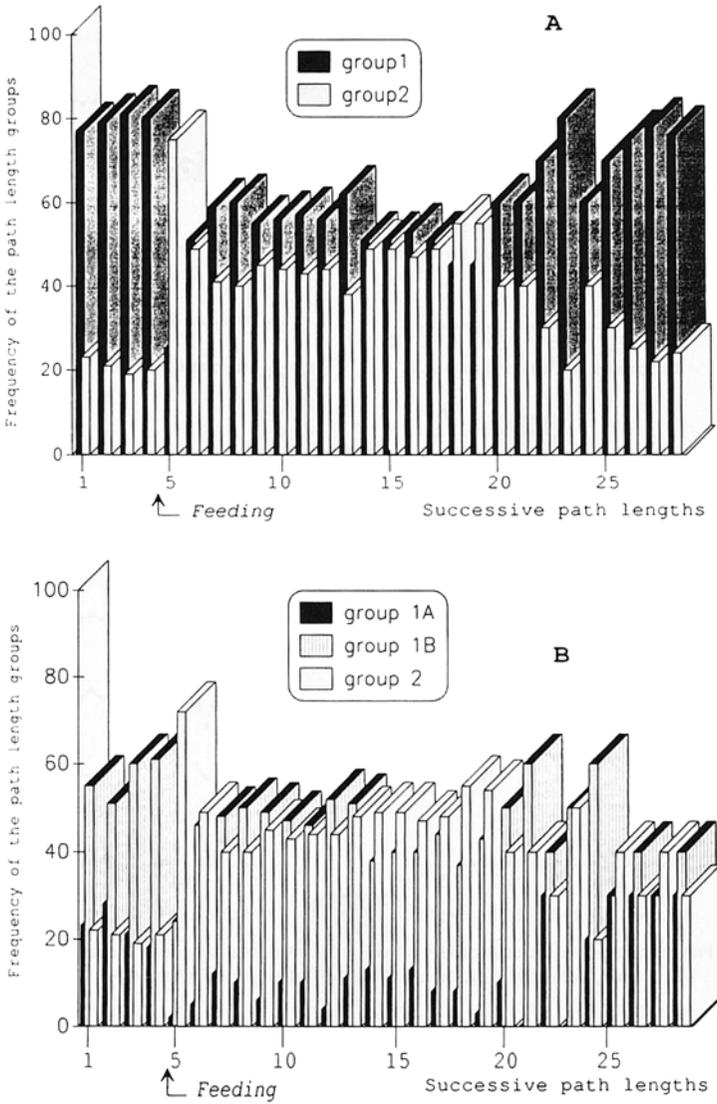
Fig. 3. Variation in movement modes and motor patterns defined by section of graph 3 at 0.5 and 0.08 levels. GR1 and GR1A, extensive search; GR1B, intermediate extensive search; GR2, intensive search.
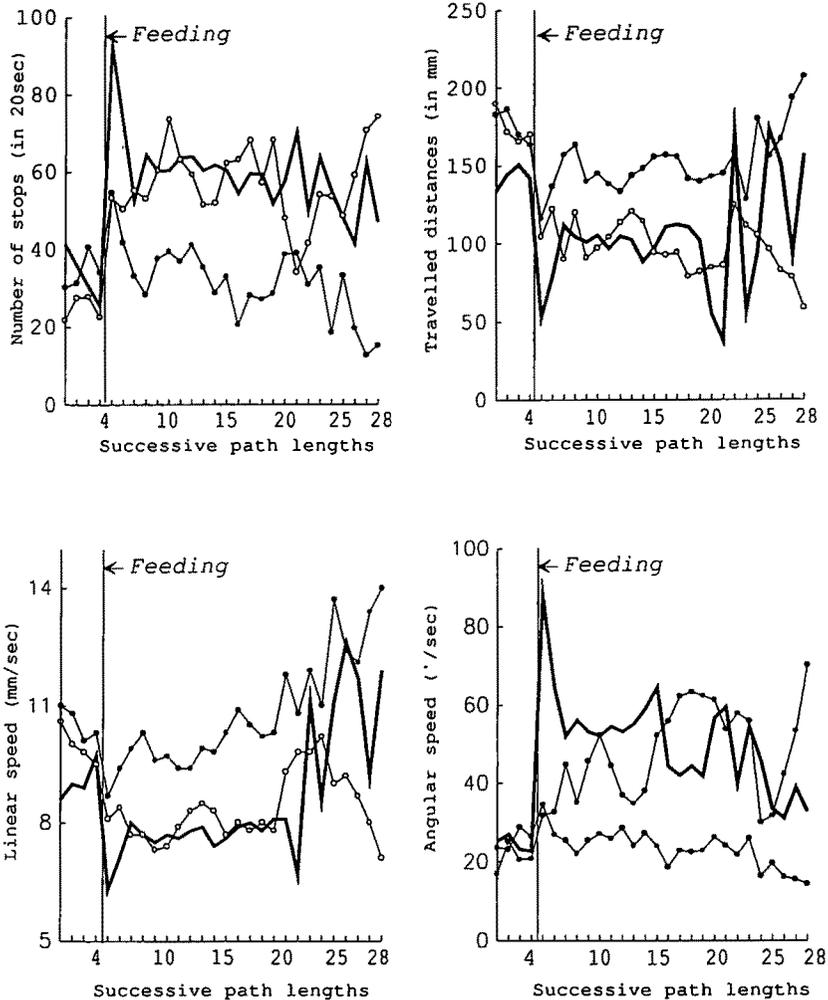
Fig. 4. Path parameter variations for larvae which adopted intensive search immediately (thick line), belatedly (○), or not at all (●) after prey consumption.

contained the 24 postfeeding path lengths (Fig. 5A) so the duration (Fig. 5B) and the number (Fig. 5C) of these periods were very heterogeneous. In consideration of these different sources of path parameter variation, it was possible to distinguish three kinds of larvae: larvae without motor response to prey consumption (11.3%), larvae with several (two to six) intensive search periods (56.4%) and larvae with only one intensive search period lasting either one path length (12.9%) or 24 path lengths (19.4%).
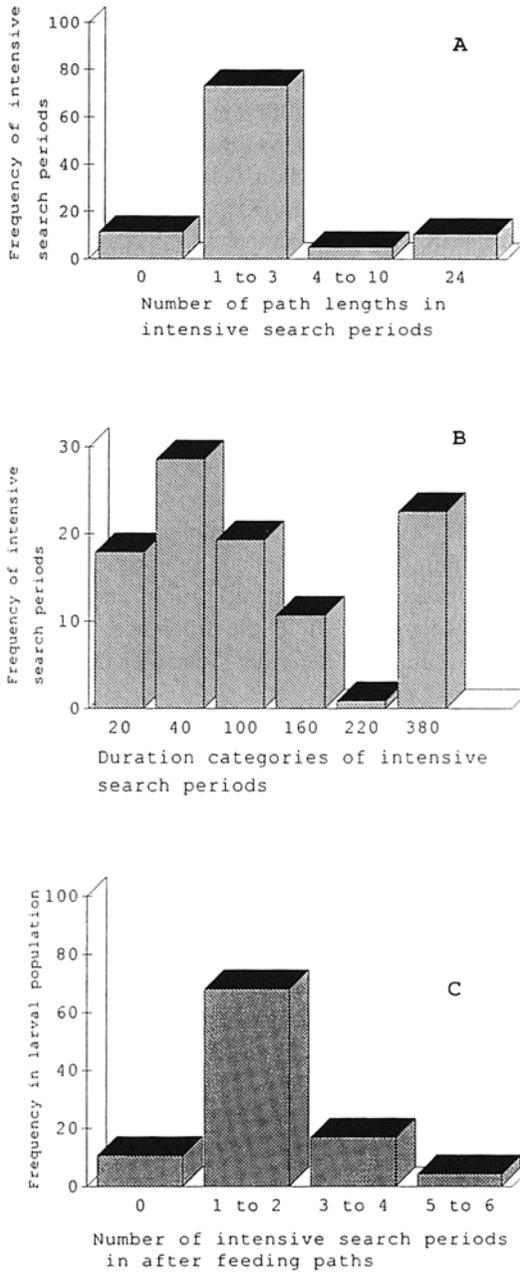
Fig. 5. Variability of periods devoted to intensive search after prey consumption according to their duration (A and B) and their number (C).

The section of the graph representing the hierarchical classification of the path lengths at the second level (0.08) did not modify the previous results, particularly the presence of path lengths devoted to intensive search before prey capture and the association of the different movement modes after feeding. Before as well as after prey consumption, most path lengths classified in group 1 (extensive search) in the first section belonged to group 1B (intermediate extensive search) in the second section (Fig. 2). The frequency of path lengths devoted to intensive search was approximately the same in the two sections.

DISCUSSION

In the last-instar larvae of *S. undecimpunctata*, the number of stops, distance traveled, and linear and angular speed changed significantly before and after feeding and varied significantly between individuals. The change in path structure following feeding is similar to that described in other coccinellid larvae (Carter and Dixon, 1982; Dixon, 1959; Hunter, 1978, Murakami and Tsubaki, 1984; Nakamuta, 1984, 1985). In *S. undecimpunctata*, the intensive search duration was about 6 min (20 path lengths), as opposed to 90 s in *Coccinella septempunctata* L. (Murakami and Tsubaki, 1984) and 3 min in *Hippodamia convergens* De Geer (Hunter, 1978). These differences may be specific or may result from a greater accuracy of the video computer tracking compared to the manual method.

The path length classification allowed us to describe path variability. First, it generally held that intensive search occurred only after prey capture. However, intensive search was observed before feeding in some larvae. Starvation causes a similar change, as it favors adoption of this motor pattern before feeding (Ferran and Dixon, 1993; Mayor *et al.*, 1987). Second, intensive search was not systematically adopted by larvae as soon as feeding ceased. A significant proportion of larvae tested either had a delayed response or continued the extensive search. This variability of the response to feeding may be advantageous for the coccinellid larvae as insurance against changes in prey dispersion. It may be that postfeeding extensive search is more efficient for encountering numerous isolated preys or small patches whereas response to feeding favors utilization of densely packed prey colonies. Tortorici and Bell (1988) gave a similar interpretation of the significance of this variability in adults of *Drosophila melanogaster*. In coccinellids, prey dispersion is studied mainly for its consequences on predatory efficiency (Murakami and Tsubaki, 1984). *Coccinella septempunctata* larvae and adults are able to capture isolated aphids walking on the ground in wheat fields and these mobile preys represent 30% of the daily food intake in spring (Ferran *et al.*, 1991).

The presence in *S. undecimpunctata* of larvae with a reduced search response

to prey consumption may be compared with the behavioral movement poly-morphism found in *Drosophila melanogaster* (Bell and Tortorici, 1987; Nagel and Bell, 1987; Sokolowski, 1980, 1985). During feeding, some larvae and adults covered long distances (rovers), whereas the others made short move-ments (sitters).In coccinellids, little is known about genetic variability in search-ing behavior.

The third reason for path parameter variability after feeding resulted from the alternation of time periods devoted either to extensive or to intensive search and from the differences in the number and the duration of these time periods between larvae. The pre- and postfeeding movements seem best defined by the variation in the ratio of periods of extensive search to intensive search. The extensive search/intensive search ratio was about 4 during prefeeding periods and 0.3 immediately after feeding and then progressively returned to the higher value. This approach questions the usual interpretation of insect movements, particularly the use of individual parameters for quantifying paths and the def-inition of the time devoted to intensive search (giving-up time). For the whole coccinellid population it was possible to define giving-up time as the time elapsed from the end of feeding to the return of path parameter values with extensive search characteristics. For individual larvae, however, the giving-up time defi-nition had to be multifactorial to take into account the previous reasons for path parameter variability.

The path length classification may generate more than two motor patterns. Are these additional search patterns, which were determined by multivariate analysis, real motor patterns? It is possible to imagine that the movements of an individual predator hunting for prey, running away from danger, or leaving a path do not have exactly the same features. A more convincing example was found in *Harmonia axyridis* Pallas larvae (Coccinellidae) fed on a substitutive prey, the eggs of *Ephestia kuhniella* Zell (Lep., Pyralidae) (Ettifouri and Ferran, 1993). After feeding on the prey item on which they were reared, larvae gave up the extensive search and carried out intensive search. Although some prey-changed larvae retained the extensive search, most of them adopted an inter-mediate intensive search, but none of them the control intensive search. The appearance of these particular motor patterns in extensive or intensive search probably depends on the physiological state of the predator such as satiety or on changes in environmental conditions such as prey quality. In *Semiadalia undecimpunctata*, young larvae and adults with a prior feeding period always engage in intensive search after feeding on new prey. On the contrary, those without such experience either continue extensive search or adopt an interme-diate extensive search, but never the control intensive search (Ettifouri and Ferran, 1992).

REFERENCES

Banks, C. J. (1957). The behavior of individual coccinellid larvae on plants. *Br. J. Anim. Behav.* **5:** 12–24.

Bell, W. J. (1990). Searching behavior patterns in insects. *Annu. Rev. Entomol.* **35:** 447–467.

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

Bell, W. J., and Tortorici, C. (1987). Genetic and non-genetic control of search duration in adults of two morphs of *Drosophila melanogaster. J. Insect Physiol.* **33:** 51–54.

Benzecri, J. P. (1979). *Pratique de l'analyse des données, t. 1: analyse des correspondences, exposé élémentaire,* Dunod ed.

Bond, A. B. (1980). Optimal foraging in a uniform habitat: The search mechanism of the green lacewing. *Anim. Behav.* **28:** 10–19.

Carter, M. C., and Dixon, A. F. G. (1982). Habitat quality and the foraging behaviour of coccinellid larvae. *J. Anim. Ecol.* **51:** 865–878.

Clément, P. (1983). Un dispositif de suivi automatique des déplacements d'animaux: premiers résultats et perspective d'utilisation. *Bull. SFECA* **2:** 119–130.

Clément, P., and Luciani, A. (1985). Un système de trajectométrie automatique pour étudier la nage d'animaux planctoniques (Rotifères). *Vehr. Inter. Verein. Limn.* **22:** 3002–3006.

Coulon, P. Y., and Charras, J. P. (1983). An experimental system for the automatic tracking and analysis of rotifer swimming behavior. *Hydrobiologia* **104:** 197–202.

Curio, E. (1976). *The Ethology of Predation, Zoophysiology and Ecology 7,* Springer, Berlin.

Delcomyn, F., and Cocatre-Zielgen, J. H. (1988). Individual differences and variability in the timing of motor activity during walking in insects. *Biol. Cybern.* **59:** 379–384.

Dixon, A. F. G. (1959). An experimental study of searching behavior of the predatory coccinellid beetle *Adalia decempunctata* L.. *J. Anim. Ecol.* **28:** 259–281.

Drost, Y., Lewis, W. J., and Tumlinson, J. H. (1988). Beneficial arthropod behavior mediated by airborn semiochemical. V. Influence of rearing method, host plant and adult experience on host searching behavior of *Microlitis croceipes* (Cresson), a larval parasitoid of *Heliothis* sp. *J. Chem. Ecol.* **14:** 1607–1616.

Ettifouri, M., and Ferran, A. (1992). Influence d'une alimentation préalable et du jeûne sur l'apparition de la recherche intensive des proies chez *Semiadalia undecimnotata. Entomol. Exp. Appl.* **65:** 101–111.

Ettifouri, M., and Ferran, A. (1993). Influence of trophic conditions of rearing on intensive search emergence in *Harmonia axyridis* Pallas larvae. *Entomophaga* **38:** 51–59.

Ferran, A., and Dixon, A. F. G. (1993). Foraging behaviour of ladybird larvae (Col., Coccinellidae). *Eur. J. Entomol.* **90:** 383–402.

Ferran, A., Iperti, G., Lapchin, L., and Rabasse, J. M. (1991). La localisation, le comportement et les relations proie-prédateur chez *Coccinella septempunctata* dans un champs de blé. *Entomophaga* **36:** 213–225.

Houck, M. A. (1986). Prey preference in *Stethorus punctum* (Col., Coccinellidae). *Environ. Entomol.* **15:** 967–970.

Hunter, K. W., Jr. (1978). Searching behavior of *Hippodamia convergens* larvae (Col., Coccinellidae). *Psyche* **85:** 249–253.

Luciani, A., and Chassé, J. L. (1983). Aging in *Brachionus plicatilis*: The evolution of swimming as a function of age at two different calcium concentration. *Hydrobiologia* **104:** 141–146.

Mayor, K. L., Aracena, J. M., and Bell, W. (1987). Search duration of *Drosophila melanogaster* on homogeneous sucrose patches: Relative effects of starvation period, sucrose concentration and patch size. *J. Ethol.* **5:** 67–74.

Murakami, K., and Tsubaki, Y. (1984). Searching efficiency of the ladybeetle *Coccinella septempunctata* L. (Col., Coccinellidae). *J. Ethol.* **2:** 1–6.

Murdoch, W. W., and Marks, J. R. (1973). Predation by coccinellid beetles: Experiments on switching. *Ecology* **54:** 160–167.

Nagle, K. L., and Bell, W. J. (1987). Genetic control of the search tactic of *Drosophila melanogaster*: An ethometric analysis of rover/sitter traits in adults flies. *Behav. Genet.* **17:** 385–408.

Nakamuta, K. (1984). Aphid bo-iʃ fluid stimulates feeding of predatory ladybeetle *Coccinella sep-tempunctata* L. (Col., Coccinellidae). *Appl. Entomol. Zool.* **19:** 123–125.

Nakamuta, K. (1985). Mechanism of the switch over from extensive to area-concentrated search behavior of the ladybeetle *Coccinella septempunctata bruckii. J. Insect Physiol.* **31:** 849–856.

Sokolowski, M. B. (1980). Foraging strategies of *Drosophila melanogaster*: A chromosomal analysis. *Behav. Genet.* **10:** 291–302.

Sokolowski, M. B. (1985). Genetic and ecology of *Drosophila melanogaster*: Larval foraging and pupation behavior. *J. Insect Physiol.* **31:** 857–865.

Tortorici, C., and Bell, W. (1988). Search orientation in adults *Drosophila melanogaster*: Response of rovers and sitters to resource dispersion in a food patch. *J. Insect Behav.* **1:** 209–223.

Vinson, S. B. (1977). Behavioral chemicals in the augmentation of natural enemies. In Ridgeway, S. B. V. (ed.), *Biological Control by Augmentation of Natural Enemies*. Plenum, New York, p. 237–279.

Ward, J. H. (1963). Hierarchical grouping to optimize an objective function. *J. Am. Stat. Assoc.* **58:** 236–244.