

# Learning affects prey selection in larvae of a generalist coccinellid predator

Guy Boivin<sup>1,2\*</sup>, Caroline Roger<sup>3</sup>, Daniel Coderre<sup>4</sup> & Eric Wajnberg<sup>5</sup>

<sup>1</sup>Horticultural Research and Development Centre, Agriculture and Agri-Food Canada, 430 Boulevard Gouin, St-Jean-sur-Richelieu, QC, Canada J3B 3E6, <sup>2</sup>Department of Natural Resource Sciences (Entomology), Macdonald Campus of McGill University, 2111 Lakeshore Road, Ste-Anne-de-Bellevue, QC, Canada H9X 3V9, <sup>3</sup>Université du Québec à Montréal, C.P. 8888 succursale Centre-Ville, Montréal, QC, Canada H3C 3P8, <sup>4</sup>Université du Québec, 475 rue du Parvis, Québec, QC, Canada G1K 9H7, and <sup>5</sup>INRA, 400 Route des Chappes, BP 167, 06903 Sophia Antipolis Cedex, France

Accepted: 16 December 2009

**Key words:** generalist predator, Coccinellidae, *Coleomegilla maculata*, Coleoptera, prey rejection behaviour, optimal foraging, experience

## Abstract

Under natural conditions, generalist predatory insects have to cope with a variety of potential prey species that are not all equally suitable. Under these circumstances, learning may be adaptive if it allows adjustment to variations in resource quality and availability. Under laboratory conditions, we examined the learning ability and memory in the prey selection process of larvae of the predatory coccinellid *Coleomegilla maculata* ssp. *lengi* Timberlake (Coleoptera: Coccinellidae). Using choice tests, we studied prey rejection behaviour of *C. maculata* fourth instars towards prey of different quality and we also tested the influence of hunger and prior experience with other food types on the prey rejection behaviour of coccinellid larvae. *Coleomegilla maculata* larvae gradually changed their behaviour and rejected low-quality hosts more frequently, whereas high-quality hosts were nearly always accepted. After 48 h, the learned behaviour appeared to be partially forgotten. Hunger and experience with other food types prior to the test had little effect on the gradual change of behaviour but the quality of the food ingested influenced the initial level of prey rejection. Our results demonstrate that (1) *C. maculata* larvae can adjust their prey selection behaviour with experience to reject progressively less suitable prey, and (2) previous experience with other prey types can influence their initial preference.

## Introduction

Optimal foraging models predict that a foraging predator has to maximize its encounter rate with the most suitable and profitable prey and avoid lesser quality resource items (Stephens & Krebs, 1986). These models usually assume that a foraging individual has complete information on all aspects of its environment. However, for generalist predatory insects that can be exposed during successive generations to different prey species living in various microhabitats, recognition of specific cues to identify the most suitable prey is unlikely (Papaj & Lewis, 1993; Hirvonen et al., 1999). Under such conditions, learning, defined

in this article as a gradual change in behaviour following continued experience and which can be forgotten with time (van Baaren & Boivin, 1998), may be adaptive because it allows an individual to acquire neuronal representations of spatial environmental configurations, sensory information or associations between perceived stimuli and environmental states (Dukas, 2008) and to adapt to a variety of situations that may be encountered (Lewis et al., 1990). Learning can enable long-lived species to switch dynamically from depleted microhabitats to more profitable ones (van Alphen & Vet, 1986).

Entomophagous insects are known to use olfactory and visual cues to detect resource-rich habitats and, with experience, they can learn to associate these cues with the most profitable habitats containing suitable prey (Pérez-Maluf et al., 2008). Learning is thus likely to be an important capability to increase overall foraging efficiency. Pre-imaginal and adult learning appears to be widespread among

\*Correspondence: Guy Boivin, Horticultural Research and Development Centre, Agriculture and Agri-Food Canada, 430 Boulevard Gouin, St-Jean-sur-Richelieu, QC, Canada J3B 3E6. E-mail: guy.boivin@agr.gc.ca

phytophagous insects (Dukas & Bernays, 2000; Xue et al., 2007), parasitoids (Stireman, 2002; Baeder & King, 2004; van Baaren et al., 2005b; Dauphin et al., 2009), and social insects (Farina et al., 2005). However, the adaptive value of learning in prey selection by generalist predators has received little attention. Most experimental works report improvement in searching behaviour (Ettifouri & Ferran, 1993), capture efficiency (Guillette et al., 2009), and prey recognition in adult predators (Blois & Cloarec, 1985; Henaut et al., 1997; Guershon & Gerling, 2006) as a result of previous experiences (Dejean et al., 2003).

Papaj & Prokopy (1989) proposed that learning occurs when an individual's behaviour (1) changes in a repeatable way as a consequence of experience, (2) changes gradually with continued experience, and (3) vanishes in the absence of continued experience of the same type, or as a consequence of a novel experience or trauma. The evolution of learning depends on the predictability of the environment within or between generations (Boivin et al., 2004), learning being more likely to occur when the environment changes between generations but remains constant within a generation (Stephens, 1991).

*Coleomegilla maculata* ssp. *lengi* Timberlake (Coleoptera: Coccinellidae) is a generalist species (Hodek & Honek, 1996) that feeds mostly on aphids and pollen (Gordon, 1985). In Canada, few generations per year are observed and longevity of the adults is approximately 1 year (Hodek, 1973). Both larval and adult stages are predaceous and attack the same prey type (Hodek & Honek, 1996). Because of their lower mobility when compared with adults, coccinellid larvae generally search and exploit prey within the habitat where the female oviposited (Wratton, 1973). Prey choice in larvae is thus influenced by the habitat preference of the ovipositing female (Hodek, 1973). Most prey species exploited by coccinellids are ephemeral in time and space (Hodek & Honek, 1996) and coccinellid adults must frequently disperse and move from one microhabitat to the other to find suitable prey. Therefore, a coccinellid immature may or may not forage in the same habitat as its mother did. Hence, *C. maculata* can experience high within-generation predictability and low between-generation predictability and thus can meet the conditions set forth by Stephens (1991) for the evolution of learning. It has been shown that prey preference (Houck, 1986) and searching behaviour (Ettifouri & Ferran, 1993) of predatory coccinellids can be influenced by conditioning on a specific prey type.

Insect prey quality varies based on species, age, sex, size and parasitization status. Parasitism provokes external and internal host modifications (Vinson, 1994) that influence the suitability of a prey for a predator. The developing parasitoid immature uses the host resources

for its own development and although parasitoids can be very efficient at using host resources (Thompson, 1999), part of it is used for energy consumption and is therefore not available for a predator preying on a parasitized prey. This effect is even more important for idiobiont parasitoids whose host does not continue to feed or develop after parasitization. Discrimination could be based either on physical changes in the prey after parasitization or on the presence of external or internal marking left by the female parasitoid during or after oviposition (van Baaren et al., 1995). In *C. maculata*, larvae are known to be able to discriminate between eggs of *Trichoplusia ni* (Hübner) (Lepidoptera: Noctuidae) of different quality. Eggs that are parasitized by *Trichogramma turkestanica* (= *evanescens*) Meyer (Hymenoptera: Trichogrammatidae) gradually decrease in quality and are less accepted by *C. maculata* larvae towards the end of the parasitoid immature development (Roger et al., 2001). At the beginning of a feeding sequence, coccinellid larvae readily accepted most parasitized eggs but, after a few encounters, they increasingly rejected them whereas rejection of unparasitized eggs was rarely observed. Thus, *C. maculata* larvae prefer young eggs as prey but because the parasitoid larval development takes longer than the embryonic development of *T. ni*, parasitized eggs towards the end of the *Trichogramma* immature development are lower-quality hosts than unparasitized eggs (Roger et al., 2001). Pre-imaginal developmental time and food intake to reach adulthood increased and survival decreased when coccinellid larvae were fed with old parasitized eggs rather than with young unparasitized eggs (Roger et al., 2001).

In the present study, we tested whether the change in prey rejection behaviour resulted from learning. We also tested whether such learning behavioural process could be forgotten and we examined the influence of hunger and food type on the egg rejection behaviour.

## Material and methods

### Rearing

Colonies of *C. maculata* were initiated with adults collected in spring from overwintering sites near corn fields in Saint-Hyacinthe (72°56'W, 45°39'N), QC, Canada. They were maintained on a fresh liver-based artificial diet (Firlej et al., 2006) and on wild flower pollen at 22 °C, 70% r.h. and L16:D8 photoperiod. *Trichogramma turkestanica*, initially originating from Egypt, was reared on eggs of *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae). *Trichoplusia ni* and *Pieris rapae* (L.) (Lepidoptera: Pieridae) were reared on artificial diets, and all were maintained at 25 °C, 30% r.h. and L16:D8 photoperiod (Boivin & Lagacé, 1999). The potato aphid, *Macrosiphum euphorbiae* (Tho-

mas) (Hemiptera: Aphididae), was collected from potato fields near St-Hyacinthe and maintained in the laboratory on potato plants, cv. Norland at 20 °C, 60–70% r.h. and L16:D8 photoperiod.

### Experimental procedures

Individual fourth instar *C. maculata* were used in all experiments. They moulted 1 day before the tests were conducted and never encountered the prey used before the experiments. All experiments were carried out by offering an equal number of two egg types (high or low quality) to a single coccinellid larva. Prey offered to *C. maculata* larvae were 18 unparasitized 1-day-old *T. ni* eggs (high-quality eggs) and 18 *T. ni* eggs parasitized 8 days before by *T. turkistanica* females (low-quality eggs). Parasitism occurred within the first 12 h of egg life. The two egg types were alternately arranged on a 14 × 14 cm glass plate in a 4 × 4 cm grid using a square pattern (6 × 6) surrounded by a Fluon<sup>®</sup>-coated ring (Dupont Fluoroproducts, Wilmington, DE, USA). The tests were conducted at 25 °C and 60–70% r.h. The experiment was terminated when the larva stopped searching for a period of 15 min. Consumed eggs were immediately replaced by an egg of the same type to keep the patch quality constant. Using such an experimental set-up, three experiments were conducted.

### Experiment 1

The objective of this experiment was to demonstrate and to quantify the learning ability of coccinellid larvae by comparing the gradual rise in the proportion of rejection of low-quality prey when compared with high-quality ones. The experiment tested for the repeatability of the individual's behaviour changes, and the gradual change in behaviour with continued experience. A total of 19 coccinellid larvae, starved for a period of 24 h before the beginning of the test, were observed.

### Experiment 2

In order to evaluate the influence of hunger and food experienced previous to the test on the change of behaviour of *C. maculata* larvae, we compared three treatments: (1) 14 larvae fed with five third-instar *M. euphorbiae* (average of total weight: 0.75 ± 0.37 mg), (2) 13 larvae fed with 10 unparasitized *P. rapae* eggs (0.74 ± 0.16 mg), and (3) 19 coccinellid larvae starved for 24 h. For fed larvae, the tests began after all prey offered were consumed.

### Experiment 3

In order to test whether coccinellid larvae could forget a learned behaviour, immediately after experiment 1 (time T1), larvae were fed with artificial diet for 24 h, starved for

another 24-h period, and replaced in the same experimental conditions (18 parasitized 8-day-old eggs and 18 unparasitized 1-day-old *T. ni* eggs) (48 h after the first test: time T2).

In each experiment, we counted the number of encounters with eggs, and the number of consumed and rejected eggs. An egg was considered rejected when either (1) the encounter lasted at least 3 s and did not result in egg consumption (no alteration), or (2) the coccinellid made a hole <1 mm in diameter in the egg chorion without attempting to consume the resource within the egg. An egg was considered accepted when it was partially or totally consumed.

For each experiment, in order to determine whether encounters with each egg type were random within prey encounter sequences, we used the non-parametric statistics described by Wajnberg (1991, 1993) and used by Colazza & Wajnberg (1998), Bayram et al. (2004) and Kapranas et al. (2009). These statistics are derived from standard rank test procedures (Hajek & Sidak, 1967) and can be used to describe sequential features of the prey encounters sequence recorded. The statistics were: (1) the sum of rank position of low-quality-egg encounters (SR) showing whether low- or high-quality eggs were encountered at the beginning of a sequence; (2) the variance of the rank position of the low-quality-egg encounters (VR) showing whether low-quality eggs were encountered in the middle of the sequence; (3) the centre-group of low-quality-egg encounters (CGP) describing whether there was any pooling of low-quality-egg encounters within the sequence; (4) the centre-group of high-quality-egg encounters within the sequence (CGU) showing whether there was any pooling of high-quality-egg encounters within the sequence; and (5) the number of runs of successive encounters of the same egg type (NR) in order to detect the presence of autocorrelation between encounters of low- and high-quality eggs within a sequence. For all these statistics and in each experiment, a  $\chi^2$  test combining all coccinellids observed was carried out to statistically test each of the associated null hypotheses (see Wajnberg, 1993). Finally, for each experiment, the total number of encounters of each egg type was submitted to a Wilcoxon's signed rank test. A difference in the number of encounters per egg type could indicate that the predator detected the quality of the host prior to contact.

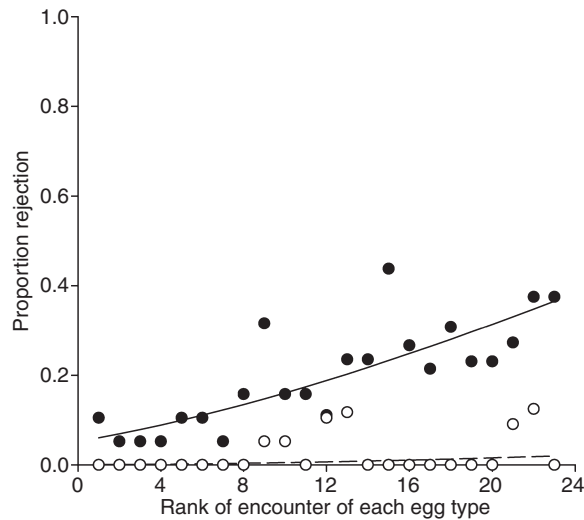
In each experiment, changes in the proportion of egg rejection in relation to the order of encounters with low- and high-quality eggs were described by linear regressions (Snedecor & Cochran, 1989). Data were first submitted to an arcsin  $\sqrt{x}$  transformation in order to homogenize the variances and were weighted by the number of repetitions for each encounter. The intercept of the regression repre-

sents the initial rejection rate of the egg type, whereas the slope represents the rate in change of behaviour. In experiment 1, the intercepts and the slopes of the regressions were compared between the two egg types. In experiment 2, the regression slopes for low-quality eggs of each treatment were compared to determine whether hunger and food quality had an influence on the change in rejection rates of low-quality eggs. In experiment 3, the regression slopes for low-quality eggs at T1 and T2 were compared to determine whether the learned behaviour had changed after a 48-h time interval. Finally, the intercept of the regression at time T2 and the point reached after 23 encounters at time T1 were compared with a Student t-test in order to evaluate whether coccinellid larvae had forgotten the learned behaviour during the 48-h interval. All computations were carried out with Proc GLM (SAS Institute, 1985).

## Results

### Experiment 1

*Coleomegilla maculata* larvae rejected high-quality eggs in proportions varying from 0.0 to 12.5%, but the proportion did not increase significantly with encounter rate (slope:  $F_{1,22} = 1.55$ ,  $P > 0.05$ ) (Figure 1). However, coccinellid larvae gradually changed their behaviour and rejected more low-quality eggs as they encountered more eggs of this type (slope:  $F_{1,22} = 36.49$ ,  $P < 0.0001$ ) (Figure 1), with 37.5% of

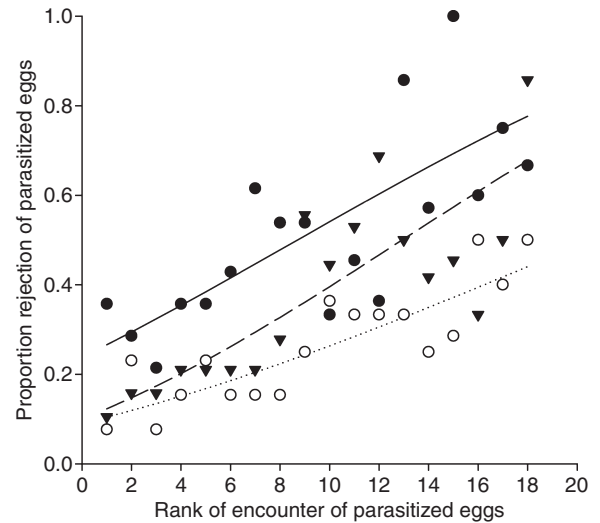


**Figure 1** Change in the proportion of rejection by *Coleomegilla maculata* of high-quality prey (dashed line, white circles) and low-quality prey (solid line, black circles). Regression equations are: on high-quality prey:  $y = 0.00548x + 0.01453$  ( $R^2 = 0.069$ ,  $P = 0.23$ ); on low-quality prey:  $y = 0.01819x + 0.23047$  ( $R^2 = 0.635$ ,  $P < 0.0001$ ). De-transformed regression lines are plotted.

the larvae rejecting the low-quality eggs after 23 encounters. The proportion of larvae that initially rejected low-quality eggs (intercept =  $5.22 \pm 0.22\%$ ) was significantly higher than the proportion observed on high-quality eggs (intercept =  $0.02 \pm 0.22\%$ ) ( $t = 3.27$ , d.f. = 45,  $P = 0.0011$ ) indicating that some innate discrimination occurred.

### Experiment 2

Larvae that were fed prior to the experiment were tested to determine whether the gradual change in rejection of low-quality eggs with encounter could be caused by satiation. The pattern of rejection was similar for fed and starved larvae (slope, fed with *P. rapae* eggs vs. starved:  $t = 1.63$ , d.f. = 35,  $P > 0.05$ ; fed with *M. euphorbiae* vs. starved:  $t = 0.47$ , d.f. = 53,  $P > 0.05$ ) (Figure 2) indicating that a decrease in hunger is unlikely to explain the increasing number of low-quality eggs rejected with encounter. However, the quality of the food ingested before the experiment influenced the initial rejection rate of low-quality eggs by the larvae (Figure 2). The proportion of larvae that initially rejected low-quality eggs when fed with aphids (intercept:  $23.86 \pm 0.41\%$ ) was significantly higher than for larvae starved for 24 h (intercept:  $10.02 \pm 0.28\%$ ;  $t = 2.27$ , d.f. = 53,  $P = 0.0234$ ) or for larvae fed with *P. rapae* eggs (intercept:  $9.06 \pm 0.42\%$ ;  $t = 2.25$ , d.f. = 53,



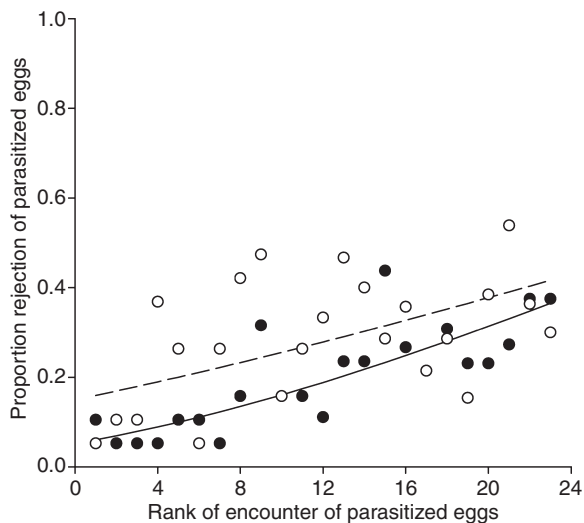
**Figure 2** Influence of starvation of *Coleomegilla maculata* (dashed line, black triangles) and food intake (*Macrosiphum euphorbiae*: solid line, black circles; *Pieris rapae*: dotted line, white circles) on the proportion of rejection of low-quality prey. Regression equations are: with starved larvae:  $y = 0.03578x + 0.32206$  ( $R^2 = 0.695$ ,  $P < 0.0001$ ); with larvae fed *M. euphorbiae*:  $y = 0.03154x + 0.51035$  ( $R^2 = 0.446$ ,  $P = 0.0024$ ); and with larvae fed *P. rapae*:  $y = 0.02330x + 0.30567$  ( $R^2 = 0.672$ ,  $P < 0.0001$ ). De-transformed regression lines are plotted.

$P = 0.0243$ ). After 18 encounters, the percentage of rejection of low-quality eggs was 77.6% for larvae fed with aphids, 67.7% for starved larvae, and 43.9% for larvae fed with *P. rapae* eggs.

### Experiment 3

To test whether, with time, the larvae are forgetting the experience acquired with encounters, the larvae used in experiment 1 (T1) were tested again after 48 h (T2). The regression slopes at time T1 and T2 were similar ( $t = 0.87$ , d.f. = 45,  $P > 0.05$ ) which indicates that coccinellid larvae learned at the same rate after a period of 48 h (Figure 3). The initial rejection rate of low-quality eggs at T2 (intercept:  $14.98 \pm 0.26\%$ ) was significantly higher than at T1 (intercept:  $5.21 \pm 0.26\%$ ) ( $t = 2.32$ , d.f. = 45,  $P = 0.0202$ ) but was significantly lower than the point reached after 23 encounters in the first experiment ( $36.5 \pm 5.60\%$ ) ( $t = 4.97$ , d.f. = 45,  $P < 0.0001$ ). This indicates that the coccinellid larvae had partially forgotten the learned behaviour after a period of 48 h.

Analysis of the sequences of low- and high-quality-host encounters by coccinellid larvae indicated that larvae showed a higher probability of encountering a low-quality egg after encountering a high-quality egg type (and vice versa) than what would be expected if sequences of host encounters were random (Table 1). This likely reflects the fact that hosts were offered to the larvae in a regular square pattern in which the two types of hosts were alternately



**Figure 3** Change in the proportion of rejection by *Coleomegilla maculata* of low-quality prey at time T1 (solid line, black circles) and T2 (48 h after T1) (dashed line, white circles). Regression equations are: T1:  $y = 0.01818x + 0.23047$  ( $R^2 = 0.635$ ,  $P < 0.0001$ ); T2:  $y = 0.01320x + 0.39748$  ( $R^2 = 0.260$ ,  $P = 0.013$ ). De-transformed regression lines are plotted.

arranged, increasing the probability of encountering a different egg type at each encounter. However, this experimental set-up did not cause an increase in the number of encounters of a specific egg type (Wilcoxon's signed rank test:  $P > 0.05$  for all situations tested) indicating that experience with each egg type was similar and that no pre-contact discrimination occurred. This is confirmed by the fact that none of the four other statistics used to describe the feature of the sequences of low- or high-quality-host encounters were significant (Table 1).

### Discussion

The present study demonstrates that larvae of *C. maculata* can learn to discriminate between prey of different quality and adjust their patch exploitation behaviour accordingly. When confronted with a mixed patch of low- and high-quality prey, *C. maculata* larvae can discriminate and select the most profitable prey based on their quality (Roger et al., 2001). Our results indicate that this discrimination ability improves with experience. *Coleomegilla maculata* larvae displayed a change in their rejection behaviour, the magnitude of which increased with successive contacts with low-quality eggs. Encounters with high-quality eggs did not induce such a change. Our results also demonstrated that this change of behaviour was partially reversible. Therefore, the three criteria of learning suggested by Papaj & Prokopy (1989) (i.e., repeatability, gradual change and reversibility) are met.

Under the conditions of our experiments, the rejection behaviour seemed to change linearly with no asymptote. This suggests that in *C. maculata*, as in other generalist insects (Maldonado et al., 1979; Johnson, 1991), learning is a rather slow process contrary to what is observed in parasitoid species (van Baaren & Boivin, 1998). Because generalist predators are frequently confronted with a diversity of food types, instantaneous recognition of specific cues associated with each food type is unlikely (Papaj & Lewis, 1993). *Coleomegilla maculata* larvae probably need several periods of exposure to the same egg type before they can adequately discriminate and adjust their foraging strategy accordingly.

Prey models predict a forager's diet when searching within a patch containing prey of different values (MacArthur & Pianka, 1966; Heller, 1980). These models are based on the capacity of a forager to recognize prey quality and modify its behaviour accordingly. If the quality of the patch decreases rapidly and density of high-quality prey becomes too low, prey selection may change and acceptance of lower-quality prey would be adaptive (Sih & Christensen, 2001), resulting in a change in the total patch exploitation duration, as shown in parasitoids (Pierre

**Table 1** Analysis ( $\chi^2$ ) of each of the five statistics used to describe the sequences of encounter with 1-day-old unparasitized and 8-day-old parasitized eggs by *Coleomegilla maculata* larvae under various conditions

Condition	d.f.	SR	VR	CGP	CGU	NR
Experiment 2, fed <i>Macrosiphum euphorbiae</i>	28	20.52 ns	26.33 ns	30.02 ns	24.02 ns	42.57**
Experiment 2, fed <i>Pieris rapae</i>	26	10.53 ns	16.25 ns	14.71 ns	15.24 ns	53.26**
Experiment 2, starved larvae	38	35.58 ns	33.87 ns	25.70 ns	35.90 ns	65.65**
Experiment 3, after 24 h	38	38.44 ns	22.30 ns	23.68 ns	23.81 ns	117.38**
Experiment 3, after 48 h	38	29.79 ns	19.19 ns	21.42 ns	22.98 ns	100.05**

All significant tests for NR are the result of significantly more runs within sequences compared with what would be expected from random sequences.

SR, sum of rank position of parasitized egg encounters; VR, variance of the rank position of the parasitized egg encounters; CGP, centre-group of parasitized egg encounters; CGU, centre-group of unparasitized egg encounters; NR, number of runs of successive encounters of the same egg type; ns, non-significant.

\*\* $P < 0.01$ .

et al., 2003). *Coleomegilla maculata* larvae searching and consuming only high-quality eggs in patches containing a high proportion of low-quality eggs would obtain a lower net energy gain when compared with larvae accepting lower quality prey. In such a case, it would be more advantageous not to be too selective.

In the absence of contact with prey for 48 h, *C. maculata* larvae partially forgot what they had learned. With experience, even generalist insects tend to specialize on a certain food type (Fox & Morrow, 1981; Papaj & Rausher, 1983) but such specialization could become detrimental if the resource becomes scarce. Forgetting previous experience could allow a foraging predator to adjust to fluctuations in food availability in a changing environment (Hirvonen et al., 1999). It is likely that memory is influenced by the duration of the exposure period to prey and by the ranking preference of prey as this was shown in parasitoids foraging for hosts (Kaiser et al., 1989; Bjorksten & Hoffmann, 1998). In generalist species, such as desert seed-harvester ants and preying mantis, it takes several days to completely forget a learned behaviour (Maldonado et al., 1979; Johnson, 1991).

It has been demonstrated in parasitoids that the physiological state and previous oviposition experience could influence their learning rate (Takasu & Lewis, 1993; van Baaren et al., 2005b) and preference (Bjorksten & Hoffmann, 1995). In the present study, hunger and experience with other food types had little effect on the rate of learning but rather changed the initial level of rejection of low-quality prey. The initial level of rejection of low-quality eggs was higher in coccinellid larvae previously fed with aphids than in starved coccinellids, but the opposite was obtained when coccinellid larvae were previously fed with *P. rapae* eggs. The preference ranking of these prey was aphids > *T. ni* eggs > *P. rapae* eggs (Hodek & Honek, 1996; C Roger, D Coderre, G Boivin, unpubl.), suggesting

that coccinellid larvae that had acquired experience on their preferential prey type became more selective in their subsequent prey searching behaviour. These results indicate that previous experience may alter the ranking of prey types and consequently may affect the selection of resource items and the patch exploitation strategy (Vet et al., 1990; van Baaren et al., 2005a).

Our study demonstrates the importance of learning in improving prey selection in a generalist predator. Results obtained support the hypothesis that, through experience, larvae could select their resource more effectively in mixed patches of prey and that learning may improve their overall foraging efficiency as shown in other insects (Punzo & Garman, 1989; Papaj & Vet, 1990; Johnson, 1991). However, our results were obtained within a single patch and sequential contacts with patches of different values, or foraging in a complex environment (Gingras et al., 2003), may change the value of learning. Finally, our results demonstrate that previous experience on other prey types can influence the initial preference of *C. maculata*.

### Acknowledgments

We would like to thank Louise Vet for useful comments on the manuscript as well as Sophie Demougeot for technical assistance. This research was supported by a grant from the Natural Sciences and Engineering Research Council of Canada (NSERC) to D. Coderre. C. Roger acknowledges support from the Fonds pour la Formation de Chercheurs et l'Aide à la Recherche (FCAR) from the Ministère de l'Éducation du Québec.

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