

## Prey discrimination by a generalist coccinellid predator: effect of prey age or parasitism?

CAROLINE ROGER,<sup>1,2</sup> DANIEL CODERRE,<sup>3</sup>  
CLÉMENT VIGNEAULT<sup>2</sup> and GUY BOIVIN<sup>1,2</sup> <sup>1</sup>Department of Natural Resource  
Sciences (Entomology), Macdonald Campus of McGill University, <sup>2</sup>Horticultural Research and Development Centre, Agriculture  
Canada and Agri-Food Canada and <sup>3</sup>Département des Sciences Biologiques, Université du Québec à Montréal, Canada

**Abstract.** 1. Patterns of prey discrimination by the generalist predatory coccinellid *Coleomegilla maculata lengi* Timb. (Coleoptera: Coccinellidae) were studied in relation to prey quality, under laboratory conditions.

2. Choice experiments were performed in which second- and fourth-instar coccinellids had the choice between *Trichoplusia ni* (Lepidoptera: Noctuidae) eggs that were young or old, unparasitised or parasitised by *Trichogramma evanescens* Westwood (Hymenoptera: Trichogrammatidae).

3. *Coleomegilla maculata* larvae did not exhibit any preference for parasitised or unparasitised eggs at a similar stage of development but always preferred younger eggs, regardless of whether or not they were parasitised. Furthermore, the percentage of rejection was higher and handling time longer on the less preferred egg type. Pre-imaginal development time, food intake to reach adulthood, and survival of coccinellid immatures were altered when coccinellid larvae were fed with parasitised and old unparasitised eggs.

4. These results indicate that *C. maculata* larvae select eggs based on their stage of development regardless of parasitism, and that prey quality of aged prey is lower.

5. Fourth-instar coccinellid larvae spent less time in patches containing solely parasitised old eggs, and their level of exploitation was greatly reduced, compared with homogeneous patches containing unparasitised young eggs. This suggests that *C. maculata* larvae respond to variable patch quality by using flexible decision rules that reflect the payoff of the patch.

**Key words.** Coccinellidae, *Coleomegilla maculata*, generalist predator, patch quality, prey discrimination, prey quality.

### Introduction

Even if they do not use the same tactics in their acquisition of resources, predators and parasitoids may compete for the same prey/host (Polis *et al.*, 1989). In several documented cases exploring predator–parasitoid interactions, generalist predators attacked parasitised hosts, consuming both the host and the immature parasitoid developing inside that host (Jones, 1987; Brower & Press, 1988; Ruberson & Kring, 1991; Hoelmer

*et al.*, 1994). Vinson (1975) was among the first to suggest that parasitoid-induced host modifications could reduce predation of parasitised prey. This was mainly observed for predators attacking sessile prey such as eggs or immature whiteflies (Al Rouechdi & Voegelé, 1981; Hoelmer *et al.*, 1994). In all cases where discrimination against parasitised prey occurred (see Rosenheim *et al.*, 1995 for review), recently parasitised and unparasitised prey were consumed in the same proportion but prey containing late larval and pupal stages of parasitoids were under-utilised.

As suggested by some authors (Al Rouechdi & Voegelé, 1981; Hoelmer *et al.*, 1994), immature parasitoids may need to reach advanced developmental stages before they can change the physiological characteristics of their hosts significantly.

Correspondence: Caroline Roger, Horticultural Research and Development Centre, Agriculture and Agri-Food Canada, 430 Boulevard Gouin, St-Jean-sur-Richelieu, PQ, J3B 3E6 Canada. E-mail: rogerc@em.agr.ca

The predator could then detect these modifications, such as changes in the texture, size, and shape of parasitised prey (Strand, 1986; Vinson, 1994), and select prey accordingly.

Many parasitoids use discrimination abilities to recognise hosts that have already been parasitised (van Lenteren, 1981; van Alphen & Visser, 1990; van Baaren *et al.*, 1994). Host discrimination has an important value for parasitoids because it prevents wastage of eggs, time, and energy (van Lenteren, 1981). Similarly, interspecific prey discrimination (i.e. to distinguish parasitised from unparasitised prey) could also enable foraging predators to evaluate prey and patch quality; however few studies have described this discrimination behaviour in predators (see Rosenheim *et al.*, 1995 for review), and none has discussed its functional significance.

The predatory coccinellid *Coleomegilla maculata lengi* Timb. (Coleoptera: Coccinellidae) was used to test the influence of parasitism on prey discrimination. This predator is one of the most abundant coccinellid species found in herbaceous crops located east of the Rocky Mountains in North America (Gordon, 1985). It is a widely polyphagous coccinellid (Hodek & Honek, 1996), feeding on many aphid species (Mack & Smilowitz, 1980; Coderre *et al.*, 1987) and various non-aphid prey such as Colorado potato beetle (Grodén *et al.*, 1990; Giroux *et al.*, 1995), and eggs and larvae of many lepidopterous species (Andow, 1990; Coll & Bottrell, 1991; Roger *et al.*, 1995). Both larval and adult stages are predaceous and attack the same prey type (Hodek & Honek, 1996). Although many coccinellids are generalist feeders, studies indicate that they are selective in their prey choice (Mills, 1981; Obrycki & Orr, 1990) and can forage in an optimal way (Hemptinne *et al.*, 1993). Discrimination ability could enable this generalist predator to cope with high variability in the quality of the numerous prey types encountered.

In this study, *Trichogramma evanescens* (Westwood) was used as the parasitoid and the cabbage looper *Trichoplusia ni* (Hübner) as the prey/host. This system has several favourable attributes for the study of prey discrimination from a functional perspective. During the acceptance behaviour, *T. evanescens* females oviposit and inject a venom responsible for the cessation of host development and necrosis. After the oviposition phase, the female deposits an external chemical mark (Strand, 1986). As a parasitoid larva develops within the host egg, it exploits the resources and secretes a surrounding membrane (Al Rouechdi & Voegelé, 1981). These physiological changes harden the egg chorion and change the egg colouration, which becomes gradually black. At the end of parasitoid larval development, most of the host resources have been used and air spaces form inside the egg (Al Rouechdi & Voegelé, 1981). Parasitised *T. ni* eggs take 9–10 days at 25 °C to complete their development whereas unparasitised eggs take 4 days. Hence, in nature, parasitised eggs are vulnerable to predation for a longer time than unparasitised eggs.

In the work reported here, the discriminatory capacity of the predator *C. maculata* was explored in a choice situation where it was presented *T. ni* eggs unparasitised or parasitised by *T. evanescens*. It is suggested that parasitism-induced modifications may alter prey suitability and change the energy and time payoffs for a foraging predator. All other constraints being

equal, if parasitised prey are less suitable than unparasitised prey, predators should have developed discrimination capacity to reduce loss of time and energy on parasitised prey.

Discrimination ability could also allow a generalist predator, such as *C. maculata*, to perceive patch quality and to exploit the encountered patches according to their relative value. To evaluate this hypothesis, the influence of prey quality on prey selection and patch exploitation was also studied. Many functional models describing patch leaving behaviour make unrealistic assumptions because they use simple fixed decision rules such as *time expectation* (leave after *t* seconds) (Gibb, 1962; Crawley & Krebs, 1992) and *number expectation* (leave after catching *n* prey) (Krebs, 1975; Crawley & Krebs, 1992) that oversimplify the constraints caused by the complexity of the environment and by the foraging activities of predators. Generalist insects confronted with a highly variable environment and differential prey suitability should be able to sample the patch and use strategies that allow them to adapt their foraging behaviour according to the quality of the resource contained in patches. In this study, the prediction included in optimal models, which states that an optimal forager should invest more time in patches with higher profitability than in those with lower profitability (Stephens & Krebs, 1986; Crawley & Krebs, 1992), was tested. If prey quality and patch variability influence the evaluation of the patch by the foraging predator, they should consequently determine patch residence time. Therefore, if parasitised eggs are of lower quality, the presence of discrimination should reduce the time spent in sites containing this egg type.

## Material and methods

### Insects

Insectary colonies of *C. maculata* were started with adults collected in spring from hibernation sites near corn fields in Saint-Hyacinthe, Québec, Canada (72°56'W, 45°39'N). They were maintained on a fresh liver-based artificial diet (D. Coderre, unpublished) and on wildflower pollen at 22 °C, 70% RH, and a LD 16:8 h photoperiod. The predatory larvae used in all behavioural experiments had moulted 2 days before the tests were conducted. Before a test, larvae were placed individually in 50 mm Petri dishes and starved for 24 h. In all experiments, coccinellid larvae were inexperienced with the prey used.

A *T. evanescens* strain, initially originating from Egypt, was obtained from the collection maintained at the Department of Entomology in Wageningen, The Netherlands (Pak & van Lenteren, 1984), and was reared on eggs of *Ephesia kuehniella* Zeller (Lepidoptera: Pyralidae) at 25 °C, 30% RH, and LD 16:8 h photoperiod. *Trichoplusia ni* larvae were reared on a pinto bean-based artificial diet elaborated by Shorey (1963) and maintained at 25 °C, 30% RH, and LD 16:8 h photoperiod. It has been shown in laboratory studies that *T. ni* eggs are a preferential host of *T. evanescens* (Parker & Pinnell, 1974) and are preyed upon readily by *C. maculata* (Roger *et al.*, 1995). *Trichoplusia ni* eggs parasitised by *T. evanescens*

**Table 1.** Egg combinations offered to second- and fourth-instar larval *C. maculata*.

Combination	Egg age (days)	Physiological state
1	18 parasitised eggs (P1)* 18 unparasitised eggs (U1)	1 1 Physiological age was equivalent for both egg types
2	18 parasitised eggs (P4)† 18 unparasitised eggs (U4)	4 4 Parasitoid immature; larval stage <i>T. ni</i> embryo; fully developed
3	18 parasitised eggs (P8)† 18 unparasitised eggs (U1)	8 1 Parasitoid immature; pupal stage (fully developed) Early in the development of <i>T. ni</i> embryo
4	18 parasitised eggs (P8)† 18 unparasitised eggs (U4)	8 4 Parasitoid immature; pupal stage (fully developed) <i>T. ni</i> embryo; fully developed
5	18 unparasitised eggs (U1) 18 unparasitised eggs (U4)	1 4 Early in the development of <i>T. ni</i> embryo <i>T. ni</i> embryo; fully developed

\* Parasitism by *T. evanescens* females occurred 1 h before observations began.

† Parasitism occurred within the first 12 h of egg life.

used in the experiments described below were parasitised within the first 12 h of egg life.

#### *Influence of parasitism and prey age on prey discrimination*

Discrimination experiments were conducted by offering a combination of equal densities of two egg types to a single second- or fourth-instar coccinellid larva without replacing consumed eggs. Eggs were arranged alternately on a 14 × 14 cm glass plate in a 6 × 6 grid with 0.8 cm between eggs in rows and columns for fourth instars and 0.4 cm for second instars. The arena was surrounded by a Fluon<sup>®</sup>-coated ring. A single coccinellid larva was observed for 1 h after the larva began to consume the first egg.

Five different combinations of eggs were used (Table 1). Combination 1 was used to determine whether *C. maculata* could detect the presence of early external or internal changes in the egg as a result of parasitism. Combination 2 was used to test whether *C. maculata* could detect the presence of a parasitoid larva inside the host egg. Combination 3 was used to evaluate whether *C. maculata* could detect the presence of parasitoid pupae and was conducted with fourth instars only. Combination 4 was used to determine whether parasitism, regardless of age, can influence prey discrimination. In both egg types of combination 4, the resources contained inside the eggs had been used up by the developing parasitoid immature in parasitised eggs and by the *T. ni* embryo in unparasitised eggs. Combination 5 tested whether age, regardless of parasitism, can influence prey discrimination. Each combination was replicated 20 times, except for combination 1, which was replicated 10 times.

The behaviour of each coccinellid larva was video-recorded and tracked automatically using an image analysis system developed for *C. maculata* (Vigneault *et al.*, 1998). For each combination and egg type, the number of encounters with eggs, the number of egg rejections, the number of eggs consumed, and the time needed to consume each egg (handling time) were recorded. An encounter was noted when a coccinellid larva

stayed in contact with the egg for more than 3 s. An egg was considered rejected when the encounter with the egg did not result in egg consumption (no alteration). An egg was considered accepted when it was partially or totally consumed. The number of eggs of each type consumed was counted at completion of each trial. Partially consumed eggs were transferred to a growth chamber and allowed to develop, but none survived.

In order to determine whether the predators accepted one of the two prey types offered preferentially, Manly's preference index (Manly *et al.*, 1972) was calculated from the number of eggs consumed:

$$\text{Manly's index} = \ln(N_e/N) / \ln(N_e^I/N^I)$$

where  $N_e$ ,  $N_e^I$  = the numbers of prey types I and II eaten,  $N$ ,  $N^I$  = the numbers of prey types I and II initially present. This index was used because it is the only method that takes into account the prey density depletion by predation during experiments (Cock, 1978; Sherratt & Harvey, 1993).

For all combinations, Manly's index of preference, the percentage of rejected eggs, and handling time were submitted to Wilcoxon's matched-pairs signed rank tests (abbreviated as Wilcoxon's MPSR) (Abacus Concepts, 1994).

#### *Influence of parasitism and age on prey suitability*

To determine whether there is a cost in eating parasitised or old *T. ni* eggs, the pre-imaginal developmental time and the number of eggs needed for *C. maculata* larvae to complete their pre-imaginal development were evaluated. *Coleomegilla maculata* eggs were obtained from insectary colonies and incubated at 22 °C, 60% RH, and a LD 16:8 h photoperiod until hatching. Neonate larvae used in this experiment were of the same age. Each larva was kept individually in a 5 cm Petri dish with wet cotton wool, and with either *T. ni* unparasitised young eggs (1 day old), *T. ni* unparasitised old eggs (3 days old), or *T. ni* parasitised eggs (8 days old) containing one or more

*Trichogramma* pupae. Each larva was fed daily with an excess of eggs (>100) throughout its immature development. This was repeated 25 times for each egg diet. Data on daily consumption and duration of pre-imaginal development on each egg diet were analysed using a one-way ANOVA followed by multiple comparisons tests (Fisher's Protected LSD) (Abacus Concepts, 1991). Chi-square tests (Abacus Concepts, 1994) were performed on the frequencies of survival to adulthood.

#### *Influence of patch quality on foraging*

The influence of patch quality on the foraging behaviour of fourth instars was investigated. The experimental design was composed of a raised 14 × 14-cm glass plate on which eggs were placed in a 7.5 × 7.5-cm grid (six rows, six columns). The glass plate was raised by 2.5 cm to allow the coccinellid to leave the arena. The plate was placed in a 50 × 50 × 25 cm plastic box to diffuse light in order to minimise the influence of phototaxis on the searching behaviour of *C. maculata*. The box was open on one side to allow for the replacement of eggs and for the observation of coccinellid behaviour. Three different patch types were used: 36 unparasitised *T. ni* eggs (1 day old), 36 parasitised *T. ni* eggs (8 days old), a mixed patch containing 18 eggs of these two categories.

Larvae were placed individually within a Fluon<sup>®</sup>-coated ring and, when the first egg was encountered and feeding had started, the ring was removed carefully. Consumed eggs were replaced immediately by an egg of the same type to avoid influence of depletion rate on patch quality. The behaviour sequences of 20 larvae for each patch type were recorded using The Observer software (Noldus Information Technology, Version 2.0, 1989). The number of encounters, the number of consumed eggs, the number of rejected eggs, the patch residence time (PRT), the giving up time (GUT), and the handling time were noted in every experiment. Patch residence time began when a coccinellid larva had started consuming its first egg and was terminated when the larva left the glass plate. Giving up time was the period between the end of the feeding bout on the last egg encountered and patch emigration (Krebs *et al.*, 1974). Experiments were conducted at 22 ± 1.0 °C and 60% RH. Each data set was subjected to a one-way ANOVA (Abacus Concepts, 1991) to test the influence of patch quality, followed by a multiple comparisons test (Fisher's Protected LSD).

## Results

#### *Influence of parasitism and prey age on prey discrimination*

The number of encounters with the two egg categories was similar in all experiments (Wilcoxon's MPSR:  $P = \text{NS}$ ), indicating that no pre-contact discrimination occurred.

Both second and fourth instars consumed unparasitised eggs (U1) and eggs that were recently parasitised (P1) in the same proportion (Wilcoxon's MPSR: second instar,  $z = -0.67$ ,  $P =$

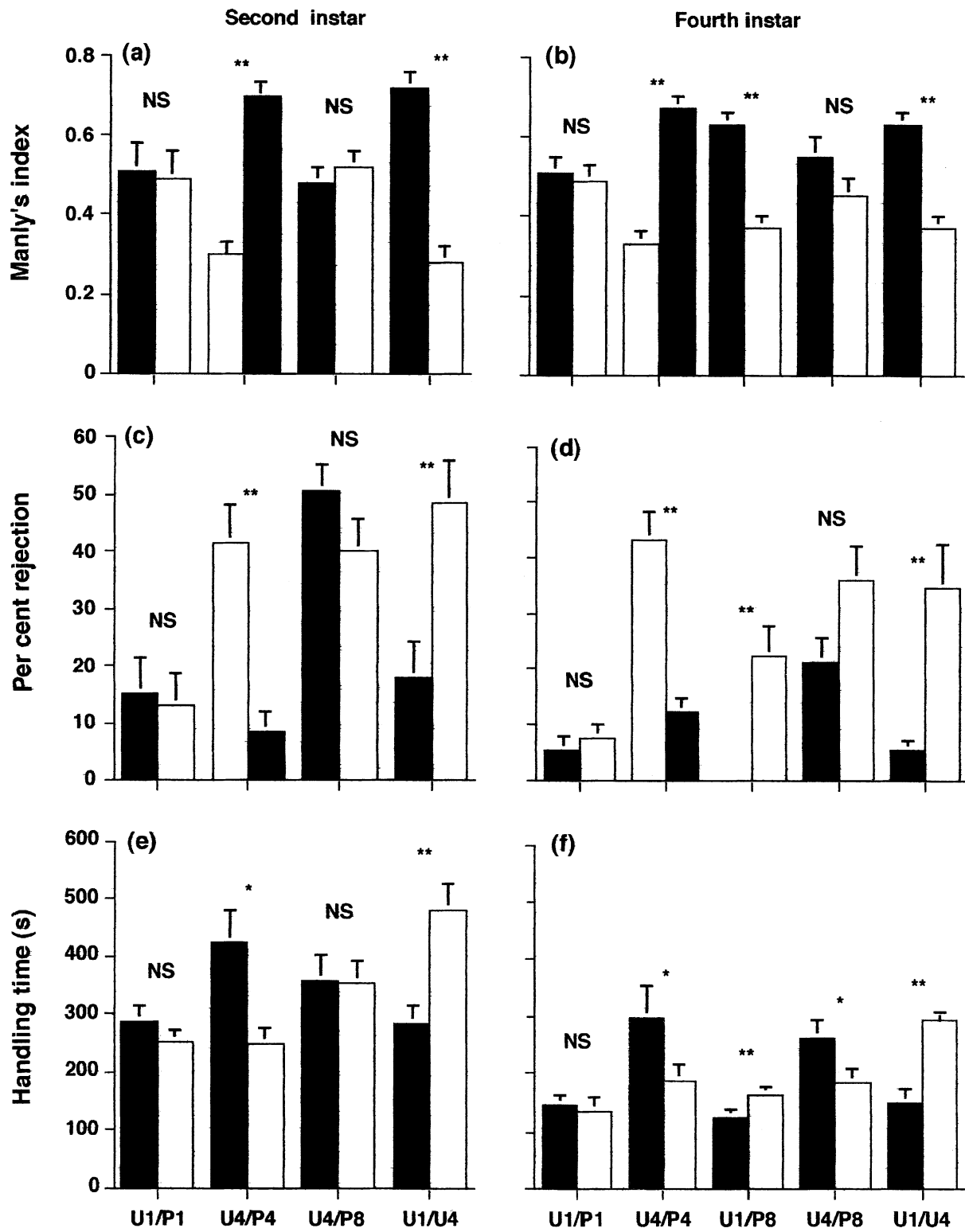
NS; fourth instar,  $z = -0.20$ ,  $P = \text{NS}$ ) (Fig. 1a,b), indicating that coccinellid larvae showed no preference for one of the prey types. There are, therefore, no indications that *C. maculata* larvae are capable of interspecific discrimination using the egg alterations provoked by the female parasitoid.

Once embryogenesis is initiated, the unparasitised *T. ni* eggs undergo more rapid physiological changes and complete their development faster (4 days) at 25 °C than do parasitised eggs (9–10 days). When confronted with unparasitised eggs at the end of their development (U4) and parasitised eggs at an intermediate stage of their development (P4), both second and fourth instars consumed a greater proportion of parasitised eggs (Wilcoxon's MPSR: second instar,  $z = -3.45$ ,  $P \leq 0.001$ ; fourth instar,  $z = -3.42$ ,  $P \leq 0.001$ ). When fourth instars had to choose between young unparasitised eggs (U1) and parasitised eggs containing a fully developed parasitoid pupa (P8), however, they preferred the unparasitised eggs (Wilcoxon's MPSR:  $z = -2.37$ ,  $P \leq 0.001$ ). Furthermore, it was noticed that fourth instars frequently opened these parasitised eggs and pulled away the parasitoid pupa without attempting to consume it or the egg chorion.

To test whether the age of eggs can influence prey discrimination, 4-day-old unparasitised eggs (U4) and 8-day-old parasitised eggs (P8) (i.e. both at the end of their development) were offered to coccinellid larvae. They were both consumed in equal proportions by second and fourth instars (Wilcoxon's MPSR: second instar,  $z = -1.82$ ,  $P = \text{NS}$ ; fourth instar,  $z = -0.91$ ,  $P = \text{NS}$ ) (Fig. 1a).

This last experiment indicates that the stage of development could be a determinant factor influencing prey selection. To evaluate this assumption, unparasitised eggs at different developmental stages were offered to coccinellid larvae. Young eggs (U1) were eaten preferentially by both second and fourth instars compared with eggs at the end of their development (U4) (Wilcoxon's MPSR: second instar,  $z = -3.42$ ,  $P \leq 0.001$ ; fourth instars,  $z = -2.95$ ,  $P \leq 0.001$ ). These results show that the stage of development of a parasitised or unparasitised egg is, in fact, the determining factor in prey selection by *C. maculata* larvae regardless of parasitism.

In combinations where discrimination was observed (Fig. 1a,b), the percentage of rejected eggs was always significantly higher on the less preferred egg type (Wilcoxon's MPSR: second instar, U4/P4  $z = -3.11$ ,  $P \leq 0.01$ ; second instar, U1/U4  $z = -2.98$ ,  $P \leq 0.01$ ; fourth instar, U4/P4  $z = -3.68$ ,  $P \leq 0.001$ ; fourth instar, U1/U4  $z = -2.85$ ,  $P \leq 0.01$ ) (Fig. 1c,d), whereas in combinations where no preference was shown, the percentage of egg rejection was equivalent for both egg types (Wilcoxon's MPSR: second instar, U1/P1  $z = -0.11$ ,  $P = \text{NS}$ ; second instar, U4/P8  $z = -1.27$ ,  $P = \text{NS}$ ; fourth instar, U1/P1  $z = -0.94$ ,  $P = \text{NS}$ ; fourth instar, U4/P8  $z = -1.78$ ,  $P = \text{NS}$ ). Similarly, in all combinations with differential egg acceptance, handling time of the less preferred eggs was always significantly longer (Wilcoxon's MPSR: second instar, U4/P4  $z = -2.41$ ,  $P \leq 0.01$ ; second instar, U1/U4  $z = -2.94$ ,  $P \leq 0.01$ ; fourth instar, U4/P4  $z = -2.80$ ,  $P \leq 0.01$ ; fourth instar, U1/U4  $z = -2.80$ ,  $P \leq 0.01$ ) (Fig. 1e,f), whereas in combinations where no preference was detected, handling time was similar on both egg types (Wilcoxon's MPSR: second



**Fig. 1.** Comparisons of mean numbers ( $\pm$  SEM) of (a,b) Manly's index of preference, (c,d) percentage of rejected eggs, and (e,f) handling time (s) between different combinations of unparasitised (U) and parasitised (P) eggs of different developmental age (number of days follows the letter of the combination). Experiments were performed with second- and fourth-instar *C. maculata*. \* $P \leq 0.05$ , \*\* $P \leq 0.01$ , NS: non-significant (Wilcoxon's MPSR test).

**Table 2.** Mean duration ( $\pm$  SEM) of pre-imaginal development, mean number of eggs consumed by *C. maculata* larvae, and percentage of survival to adulthood according to different egg diets: unparasitised 1-day-old (U1), unparasitised 3-day-old (U3), parasitised 8-day-old (P8). In a column, means followed by the same letter are not significantly different,  $P > 0.05$  (Fisher's PLSD tests).

Diet	Mean duration (days)	Mean number of consumed eggs	Percentage survival
U1	24.65 $\pm$ 0.31a	83.72 $\pm$ 2.47a	72.0a
U3	23.83 $\pm$ 0.35a	100.20 $\pm$ 2.54b	48.0a
P8	25.75 $\pm$ 0.39b	120.80 $\pm$ 1.43c	48.0a
Tests	ANOVA $F = 6.84$ ( $P \leq 0.01$ )	ANOVA $F = 61.80$ ( $P \leq 0.001$ )	Chi square $\chi^2 = 3.00$ ( $P = 0.08$ )

instar, U1/P1  $z = -1.84$ ,  $P = \text{NS}$ ; second instar, U4/P8  $z = -0.28$ ,  $P = \text{NS}$ ; fourth instar, U1/P1  $z = -0.15$ ,  $P = \text{NS}$ ). In the U4/P8 combination, however, the handling time of fourth instars was shorter on unparasitised eggs (Wilcoxon's MPSR:  $z = -2.60$ ,  $P \leq 0.01$ ), even though the two egg types were eaten in the same proportion (Fig. 1b). Generally, the discrimination ability of young (second instar) and old (fourth instar) *C. maculata* larvae was similar for all egg combinations.

#### Influence of parasitism and age on prey suitability

To determine the energetic returns associated with eating parasitised or old unparasitised eggs, the pre-imaginal developmental time, the number of eggs needed for coccinellid larvae to complete their immature development, and their survival were evaluated (Table 2). *Coleomegilla maculata* required a greater number of parasitised eggs (P8) to complete its pre-imaginal development and took significantly more time on this diet to reach the adult stage compared with immatures provided with unparasitised young *T. ni* eggs (U1). Duration of pre-imaginal development was similar for immatures reared on young (U1) and old (U3) unparasitised eggs, however the mean number of old unparasitised eggs (U3) needed to complete larval development was significantly higher compared with young eggs (U1) but lower compared with parasitised eggs (P8). The percentage of individuals that reached adulthood did not differ significantly among the three diets even though a higher survival rate was noted on the diet of young *T. ni* eggs (U1). Young *T. ni* eggs (U1) are therefore more suitable than older unparasitised eggs (U3) or parasitised eggs (P8) for the development of *C. maculata*.

#### Influence of patch quality on foraging

When it detects parasitised prey, a coccinellid larva should be able to reduce its searching effort to a degree that reflects the reduced payoff of the patch. In this experiment, fourth instars were allowed to search in a patch containing only parasitised eggs (P8), only unparasitised eggs (U1), or both egg types (U1/P8). Fourth instars stayed for a longer time (ANOVA

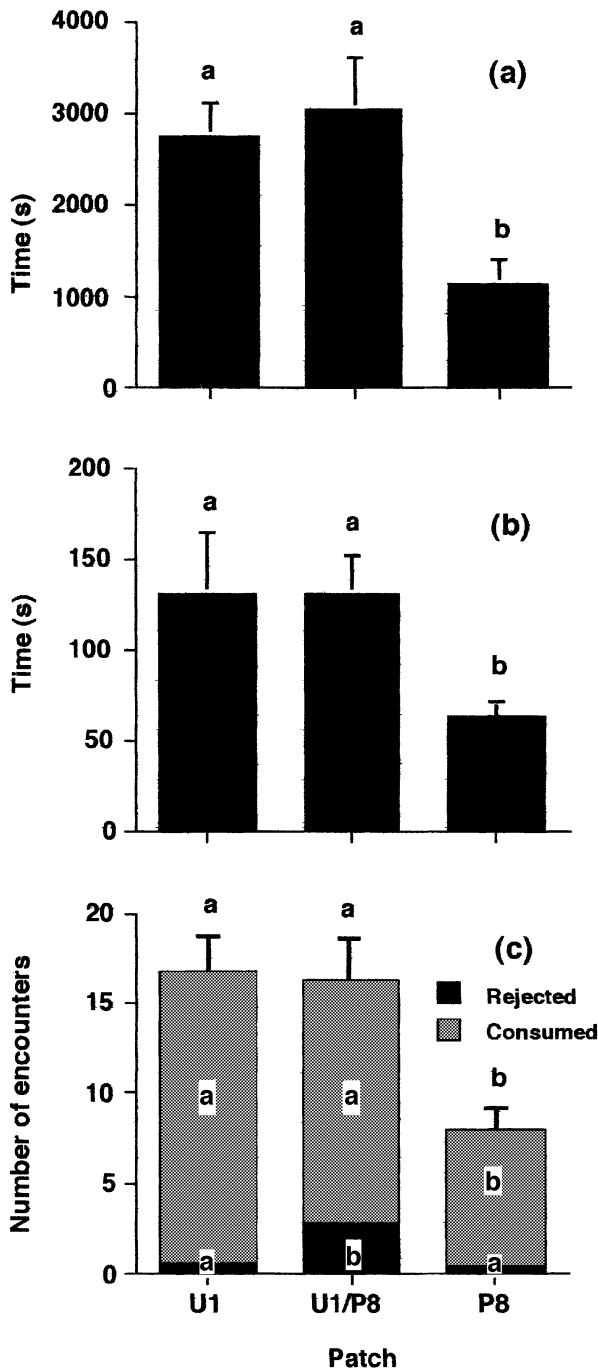
$F = 6.37$ ,  $P \leq 0.01$ ) and gave up less rapidly after the last egg encounter ( $F = 3.85$ ,  $P \leq 0.05$ ) in a patch containing only unparasitised eggs or in a mixed patch of unparasitised and parasitised eggs than larvae searching in a patch containing only parasitised eggs (ANOVA  $F = 6.01$ ,  $P \leq 0.01$ ) (Fig. 2). Consequently, the level of patch exploitation was reduced significantly for patches containing only parasitised eggs (Fig. 2c). The mean number of encounters with eggs (ANOVA;  $F = 4.10$ ,  $P \leq 0.05$ ) and the mean number of consumed eggs (ANOVA  $F = 3.93$ ,  $P \leq 0.05$ ) were 50% lower in parasitised patches; however fourth instars searching in mixed patches rejected significantly more eggs than fourth instars confronted with eggs in homogeneous patches (ANOVA  $F = 6.86$ ,  $P \leq 0.01$ ) (Fig. 2c). Most (>90%) of the rejected eggs in mixed patches were parasitised.

Another factor that could play an important role in patch exploitation by coccinellid larvae is the differential handling time observed on both egg types in mixed patches compared with the corresponding handling time in homogeneous patches (Table 3). When confronted with both egg types simultaneously, fourth instars spent more time handling parasitised eggs than unparasitised eggs, whereas in homogeneous patches, handling time was similar for both types of eggs. Nevertheless, longer handling times of parasitised eggs and time lost in egg rejection by fourth instars in mixed patches did not affect their level of exploitation significantly compared with homogeneous unparasitised patches (ANOVA  $F = 3.93$ ,  $P = \text{NS}$ ) (Fig. 2c).

## Discussion

In nature, even if most coccinellids feed on a wide range of prey types (Hodek & Honek, 1996), their prey are not always of equivalent value (Smith, 1965; Mills, 1981; Obrycki & Orr, 1990). As predicted by optimal foraging models, predators searching for prey should select the most profitable prey type and reject unprofitable prey (Crawley & Krebs, 1992). Such decisions minimise loss of opportunity time and maximise energy return (Stephens & Krebs, 1986). Therefore, if parasitism alters prey suitability and profitability, the detection and recognition of a mark left by a parasitoid female or of morphological and physiological changes provoked by a developing parasitoid immature, would have strong advantages for a predator.

Results presented here showed that *C. maculata* larvae did not exhibit any preference between parasitised and unparasitised eggs at a similar stage of development, whether they were young or old eggs. Hence, even if *C. maculata* larvae detected that its prey had been parasitised, it did not affect prey choice. In contrast, most studies have shown that egg predators avoid parasitised prey containing parasitoid larvae or pupae (Al Rouechdi & Voegelé, 1981; Brower & Press, 1988; Ruberson & Kring, 1991; Hoelmer *et al.*, 1994). It has been suggested that the differential preference observed is a function of the physiological changes provoked by the developing parasitoid (Fritz, 1982). These changes harden the chorion and decrease the availability of the resource, making it more difficult to



**Fig. 2.** Mean ( $\pm$  SEM) (a) patch residence time, (b) giving-up time, and (c) number of encounters with eggs by fourth-instar *C. maculata* in patches containing only unparasitised eggs (U1) or parasitised eggs (P8) or in patches with an equal density of both egg types (U1/P8). Different letters indicate significant differences at  $P \leq 0.05$  (ANOVA followed by a Fisher's PLSD test).

penetrate the egg and obtain food (Al Rouechdi & Voegelé, 1981; Ruberson & Kring, 1991). Despite these changes, however, handling time of parasitised eggs containing late

**Table 3.** Mean handling time ( $\pm$  SEM) of unparasitised and parasitised eggs in a mixed patch and in a patch containing only one of the two egg types. In a row, means followed by the same letter are not significantly different,  $P > 0.05$  (Fisher's PLSD tests).

Patch	Mean duration (s)		ANOVA
	Unparasitised	Parasitised	
Homogenous	112.14 $\pm$ 4.01a	117.12 $\pm$ 3.54a	$F=0.645$ ( $P > 0.05$ )
Mixed	129.23 $\pm$ 6.50a	172.70 $\pm$ 12.65b	$F=10.976$ ( $P \leq 0.05$ )

parasitoid stages was no longer than the handling time of unparasitised eggs near eclosion. This suggests that the physiological changes occurring within old parasitised eggs did not render these eggs more difficult to manipulate than old unparasitised eggs and that it did not stop both second and fourth instars from gaining access to the egg resource; however the larvae frequently left aside parts of the eggs and often removed the parasitoid pupae without attempting to consume them, a behaviour also observed by Wheeler *et al.* (1968) in a study involving *C. maculata* attacking parasitised aphids.

These results suggest strongly that *C. maculata* larvae select prey based on the physiological changes caused by the embryo, regardless of parasitism. Generally, the quality of the egg resource decreases with age (Vinson, 1994). As the embryo develops, the stored resources within the egg decrease and the embryonic tissues become more complex (Pak, 1986; Vinson, 1994). Ruberson *et al.* (1987) suggested that, in the case of developing parasitoid larvae, these changes may reduce the accessibility and suitability of an egg. Many studies of host suitability for oophagous parasitoids indicate that parasitoid females usually select younger eggs and that it corresponds to higher suitability for parasitoid immature development (Juliano, 1982; Hintz & Andow, 1990; Ruberson & Kring, 1993). Similarly, age could also alter egg suitability for coccinellid larvae and this reduced suitability might explain the prey choice observed. Furthermore, it is expected that both parasitoid larvae and *T. ni* embryos would alter egg suitability in a similar way as both use the egg resources to complete their development. The findings reported here support this hypothesis because old parasitised and unparasitised eggs were less suitable for the development of *C. maculata* immatures. Developmental time and the number of eggs needed for *C. maculata* to complete its development were higher on both old parasitised and old unparasitised eggs, and survival to adulthood was greatly reduced on both egg types.

Egg profitability decreases with age as the developing embryo gradually uses the resources within the egg. As described in the optimal diet model (Crawley & Krebs, 1992), profitability is defined as a ratio of the energetic value to the time required to pursue and consume that prey (handling time). In the experimental design used in the present study, as eggs were placed in a regular grid, it is assumed that searching time on both egg types was similar; however a longer handling time on older eggs due to the alterations provoked by the

developing *T. ni* embryo or by the parasitoid immature is expected. The results support this prediction as handling time increased with egg age. A similar increase in handling time has been observed with ovipositing parasitoid females (van Huis *et al.*, 1991; Ruberson & Kring, 1993). Hence, even if the energetic value of young and old eggs is equal, it is probable that the profitability of old eggs is lower due to higher handling time. Overall, egg preference by the generalist predator *C. maculata* was related to egg suitability and to their costs in terms of lost opportunity time.

An important role of prey discrimination is to perceive patch quality and adjust patch residence time to exploit the patch according to its relative quality. Models, principally elaborated for parasitoids, propose that a female parasitoid should allocate more time to the exploitation of a patch perceived as being of good quality (Waage, 1979; McNair, 1982). Similarly, it can be expected that a predator with discrimination ability will invest its patch searching and exploitation time according to patch profitability. Flexible patch residence time and giving up time would determine the payoff of different patch qualities (van Alphen & Galis, 1983). Coccinellid larvae left the patch and gave up more rapidly after the last egg encounter when the patch contained only parasitised eggs compared with homogeneous unparasitised patches, resulting in a patch exploitation 50% lower in parasitised patches. These results suggest strongly that *C. maculata* larvae respond to variable patch quality by using flexible decision rules based on discrimination ability rather than fixed rules, and that the decisions reflect the different patch quality.

After the consumption of the first egg, coccinellid larvae usually adopted an intensive search pattern that involved slow and sinuous movements. Leaving the patch was preceded by a switch to extensive search that involved faster linear movement, a searching behaviour observed in many other coccinellid species (Dixon, 1959; Nakamuta, 1982). For such predators that use a searching pattern adapted to patchily distributed prey (Dixon, 1959; Nakamuta, 1982), it may not be optimal to be highly selective in prey choice when prey are relatively scattered, as *T. ni* eggs usually are in nature (Harcourt, 1962; Shorey *et al.*, 1962). Furthermore, costs associated with travel and increased risk of predation associated with searching a new patch may outweigh the benefits associated with finding a better patch (Charnov, 1976; Stephen & Krebs, 1986). With such constraints, it might be more appropriate for a predator like *C. maculata* to spend more time in patches containing prey of lower quality rather than leaving the patch to search for a higher quality patch. The results obtained here corroborate these assumptions because *C. maculata* larvae allocated similar periods of time to prey search in both heterogeneous patches and patches containing only good quality prey. There were no significant differences between the exploitation rates of the two patch types even though coccinellid larvae had to discriminate and reject parasitised eggs. The frequency of adequate host discovery in mixed patches was probably above the threshold at which a larva would switch from intra-patch intensive search to inter-patch extensive search.

Little is known of the mechanisms underlying prey discrimination by coccinellids. Rejection of parasitised eggs occurred only after *C. maculata* larvae had contacted and probed the egg, as in the case of other egg predators (Al Rouechdi & Voegelé, 1981; Brower & Press, 1988; Ruberson & Kring, 1991), or after making a small hole in the egg. This recognition ability allows the predator to locate and exploit suitable eggs and to save time on less suitable eggs. Morphological and physiological changes caused by ageing are exploitable cues for parasitoids that can be used to recognise and assess host quality (Strand, 1986; Vinson, 1994). Similarly, in studies involving predators confronted with sessile parasitised prey, it has been suggested that changes provoked by a developing parasitoid immature (Al Rouechdi & Voegelé, 1981; Hoelmer *et al.*, 1994) could be detected by a foraging predator. In both types of homogeneous patches, the percentage of rejected eggs and handling time were similar whereas in heterogeneous patches, a higher percentage of rejected eggs and longer handling times were observed on parasitised eggs. This could indicate that in heterogeneous patches, *C. maculata* larvae could detect modifications in the chorion structure and associate them with the egg type of lower quality. These changes may signal to the predator that egg resource quality has decreased to an unacceptable level (Vinson, 1994), provoking a decrease of motivation to consume the less suitable prey type. This phenomenon has also been observed in parasitoid females that adjust the sex ratio of their progeny according to different host sizes present in the patch, whereas in patches containing only one host size, the progeny allocation holds constant (Kring, 1993).

This study suggests that age structure of both prey and parasitoid populations plays a significant role in prey selection by *C. maculata* in the field.

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