



Differential prey utilization by the generalist predator *Coleomegilla maculata lengi* according to prey size and species

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Abstract

Prey utilization by the generalist predator *Coleomegilla maculata lengi* Timb. (Coleoptera: Coccinellidae) of three sympatric lepidopterous species was quantified in relation with prey size (age) and prey species. Based on optimal foraging theory, we argued that costs associated with the utilization of small and large prey are higher than those of intermediate prey size. As a result, we expected a higher prey consumption rate on intermediate prey size leading to a convex prey consumption curve. Laboratory experiments showed that, within a given prey instar, *Coleomegilla maculata lengi* preyed more on *Plutella xylostella* (L.) compared to *Artogeia rapae* (L.) and *Trichoplusia ni* (Hübner). Generally, prey consumption rate by *Coleomegilla maculata lengi* on the three prey species decreased with increasing immature prey size (age). The predation efficacy of *Coleomegilla maculata lengi* adults and fourth instar larvae was higher compared to younger coccinellids (L2). Although, *Coleomegilla maculata lengi* showed a higher level of predation on smaller immature prey, we demonstrated that it is not the optimal size range for this predator. As predicted, prey weight consumption rate by *Coleomegilla maculata lengi* was higher at intermediate prey size leading to a convex prey utilization curve. The beneficial impact of *Coleomegilla maculata lengi* predation on the host plant was also estimated by using a Protection Index that considers the differential predation caused by the coccinellids and the relative importance of each pest species in terms of plant injury. *Coleomegilla maculata lengi* has a more significant beneficial impact when it preys on *T. ni* immatures.

Introduction

Generalist predators are confronted with a variety of prey types which differ in energetic values and costs associated with their capture and ingestion. Hence, even if the energetic value of a prey is a key factor in prey selection, foraging predators face several constraints that may influence their net energy gain and, consequently, prey profitability (ratio of energy gain to costs associated with searching and consuming a prey) (Krebs & McCleery, 1984). Optimal foraging theory (Stephens & Krebs, 1986) assumes that predators utilize the different prey types available so

as to maximize their rate of energetic gain. It has been usually assumed that the energetic value and the encounter rate are a function of prey size and, therefore, predators should preferentially utilise larger prey (Charnov, 1976). However, prey-predator and host-parasitoid studies have shown that capture success rate may decrease with increasing prey size because of better defense responses or escape abilities of larger prey (Pastorok, 1981; Chau & Mackauer, 1997). These defense responses may increase the mortality risk of predators as well as the handling time of prey (Pastorok, 1981; Sabelis, 1992) and, in return, decrease profitability of larger prey. Consequently, it should be

more advantageous to attack and utilise smaller prey even if larger prey offer a higher energetic gain. Prey detection, mobility and rapidity of predator response following prey contact are constraints that may also strongly influence the capture success rate of predators (Malcolm, 1992).

Even if the constraints associated with the utilization of small and large prey are different, we hypothesize that, at both ends of the size spectrum, predators experience a decrease in their rate of energy gain. We therefore predict that (1) the prey consumption rate will be higher on intermediate prey size leading to a convex prey consumption curve. Because costs associated with handling time and risk of injury decrease with increasing predator size (Sabelis, 1992), we also predict (2) that the prey consumption rate of larger predators will be higher. As the effectiveness of behavioural defense responses also varies with prey species (Dixon, 1958; Hajek & Dahlsten, 1987; Chau & Mackauer, 1991), we further hypothesize that (3) interspecific differences in morphology, mobility and behavioural defense capacity will modulate the prey consumption curve of the predator.

The predaceous coccinellid *Coleomegilla maculata lengi* Timb. is a nearctic polyphagous species (Hodek & Honek, 1996). All four instars, as well as the adult, are predaceous and may attack the same prey type. Although many coccinellids are generalist feeders, predation studies indicate that they may also be selective in their prey choice (Mills, 1981; Obrycki & Orr, 1990). *Coleomegilla maculata lengi* has been reported feeding on aphids (Mack & Smilowitz, 1980; Coderre et al., 1987), eggs of the European corn borer (Andow, 1990; Coll & Bottrell, 1991), and eggs and young larvae of Colorado potato beetle (Grodén, 1990; Giroux et al., 1995). It may also complete its development on pollen of several plants (Smith, 1960; Hodek et al., 1978). This species could be used as a biological control agent based on its capacity to rely on alternate prey during periods of low density of the target prey (Hodek, 1993).

Predatory coccinellids, while searching for prey, orient themselves through taxes (phototaxis and geotaxis) and plant structure (Hodek, 1993). Adults respond to visual cues (Meredia et al., 1992; Lambin et al., 1996) but only from very short distances (Stubbs, 1980; Hattingh & Samways, 1995) whereas prey location in larvae occurs only upon physical contact (Dixon, 1959; Storch, 1976). Compared to larvae, adult coccinellids are known to have higher mobility (Wratten, 1973), higher efficiency for prey

detection (Lambin et al., 1996) and higher capture success rate (Dixon, 1959). These factors often vary according to prey species (Dixon, 1959; Hajek & Dahlsten, 1987). Hence, predator age, prey size and their escape or defense responses may play an important role in prey utilization for a coccinellid facing different prey types in their habitat. Although much information is available on the types of behaviour related to searching, pursuing, capturing and eating, very little is known about the behaviour related to prey size or prey species. In southwestern Québec, *Coleomegilla maculata lengi* was found to be the most abundant predator in crucifers (Roger et al., 1995) but little is known on its prey range and possible impact on the lepidopterous species occurring in these cultures. In a study realized in New York state, Pimentel (1961a) also noted that *Coleomegilla maculata lengi* was a major aphid predator on crucifers and suggested that it contributed to the control of caterpillars (Pimentel, 1961b) but the predation efficacy of the coccinellid was not quantified. Three sympatric lepidopterous species are present in crucifers in southwestern Québec, the imported cabbageworm, *Artogeia* (= *Pieris*) *rapae* (L.), the diamondback moth, *Plutella xylostella* (L.) and the cabbage looper, *Trichoplusia ni* (Hübner). These species are of different sizes, have different morphologies and exhibit different locomotion behaviour. These differences in sizes and feeding habits translate into differences in the level of damage these pests can cause (Shelton et al., 1982). Injury equivalencies for the three species have been established (Harcourt et al., 1955) and they are expressed in Cabbage Looper Equivalents (CLE). This index has been used to quantify the impact of each lepidopterous species on different plants in order to calculate more precise intervention levels (Shelton et al., 1982; Dornan et al., 1994). In a tritrophic perspective, the combination of the CLE index and the different prey utilization rates of the predator *Coleomegilla maculata lengi* could allow a better understanding of the effect of predator-prey interactions on primary production of the host plant.

The purpose of this investigation was to determine the influence of prey size, prey species and predator age on prey utilization by the polyphagous predator *Coleomegilla maculata lengi* under laboratory conditions. The beneficial effect of predation on the host plant was also evaluated using a Protection Index (PI) that considered the differential mortality caused by *Coleomegilla maculata lengi* on the three lepidopter-

ous species and the relative importance of each pest species in terms of plant injuries.

Methodology

Insects. Adult *Coleomegilla maculata lengi* were collected in early May from hibernation sites near corn fields in Saint-Hyacinthe (72°56'W, 45°39' N), Québec, Canada. They were kept on a fresh liver-based artificial diet (Coderre, unpubl.) and on wild flower pollen at 22 °C, 70% r.h., and a photoperiod of L16:D8. Eggs were collected twice a week and put in Petri dishes until hatching. Larvae were also fed with the liver-based diet and pollen. The predatory larvae used in the experiments had molted two days before the tests were conducted. Before a test, adults, second and fourth instar larvae were placed individually in 50-mm Petri dishes and starved for 24 h to standardize hunger level.

Eggs and larvae of the three lepidopterous species were reared at 25 °C, 60% r.h., and a photoperiod of L14:D10 on an artificial diet specific to the needs of each species. These artificial diets were developed by Webb & Shelton (1988) for *A. rapae*, by Shelton et al. (1991) for *P. xylostella* and, by A.M. Shelton (pers. comm.) for *T. ni*. All eggs used in the experiments were less than 24 h old. All larvae were used 24 h after entering a specific instar and were identified using morphological characteristics described by Richards (1940) and Harcourt (1957, 1962).

Differential predation. Prey utilization was measured using non-choice tests in which second and fourth instar larvae as well as adults *Coleomegilla maculata lengi* were individually placed in the presence of either eggs, first-, second-, or third-instar larvae of each lepidopterous species. Preliminary tests have indicated that neither larvae or adult *Coleomegilla maculata lengi* were able to consume fourth-instar larvae of *A. rapae* and *T. ni*. Consequently, this instar was not included in the experiment. Twenty replicates were conducted for every predator-prey combination. Each coccinellid was offered a number of prey, determined in preliminary tests, that varied between 30 and 200 eggs or between 3 and 35 larvae according to predator and prey sizes. To minimize potential interference on prey utilization due to the decrease of prey availability, prey were offered in excess. The appropriate number of prey was placed on a leaf of cabbage (Prime blue Y.R. 65-3540) of

approximately 7 cm in diameter in a plastic container (11 cm in diameter and 2 cm in depth). The stem of the leaf was inserted in the side of the container, the hole was sealed with plasticine and a wet piece of cotton was placed around the stem to prevent leaf desiccation. The prey were allowed to settle before a predator was placed on the cabbage leaf. A piece of muslin held by a rubber band was used to close the system. The leaf was not in contact with the muslin nor the bottom and sides of the container allowing the prey and the predator to move freely. Therefore, the prey did not have access to a refuge but they could elude predator attacks by using escape responses. Five containers without predators were included in each predator-prey combination as experimental controls. A complete randomized block design was used which included all predator-prey combinations with replications in time. Experiments were held at 22 °C, 70% r.h., and a photoperiod of L16:D8.

After 24 h, mortality as determined by broken chorion for eggs or by death of larvae, was evaluated. To correct for mortality of prey unrelated to predation, mean mortality observed in controls was subtracted from mean mortality in the corresponding experimental treatments (Lucas et al., 1997). Partial consumption of prey was included in the evaluation of fresh weight consumption. Square root transformed data were subjected to a 3-way ANOVA (SuperAnova, Abacus Concepts, 1991) to test the influence of prey species, prey age, and predator age. When interactions between factors occurred, simple contrasts within the global model were performed. Prey capture efficacy of *Coleomegilla maculata lengi* defined as the percentage of predators that was successful in attacking and consuming at least one prey, was also evaluated. Chi-square tests (StatView, Abacus Concepts, 1994) were used to verify the influence of prey size, prey species, and predator age on *Coleomegilla maculata lengi* capture efficiency.

Weight of *Coleomegilla maculata lengi* was determined by weighting 10 live individuals of each predator stage tested. Average weights obtained were submitted to a One-way ANOVA to evaluate the differences between predator stages.

Prey weight consumption. Mean weight of each stage of the three lepidopterous species was evaluated by weighting live individuals. Twelve replicates containing 50 eggs, 20 first-, 10 second- or 5 third instar larvae of each prey species were conducted. Average weights obtained were analyzed using a 2-

way ANOVA to determine if there were prey weight differences between prey species and prey stages.

In order to determine the rate of prey weight consumption by larvae, the number of prey consumed was transformed to prey weight consumption by multiplying the average weight of each prey stage by the number of prey partially or totally consumed by each predator. To evaluate the effect of prey body size on the utilization success rate of *Coleomegilla maculata lengi*, we related the results of prey weight consumption for all three lepidopterous species to the weight of each prey stage offered. These data were submitted to linear and parabolic regressions (StatView, Abacus Concepts, 1994) to evaluate the relation between the two variables.

The number of successful attacks needed for a coccinellid predator to consume 1 mg in prey weight was estimated using the data obtained in the predation experiments (number of prey killed in 24 h) divided by the prey weight consumption rate for each predator-prey combination (Table 1).

Impact of predation on plant damage. The potential impact of predation by *Coleomegilla maculata lengi* on the primary production of the host plant was evaluated by using a Protection Index (PI). This index considers the number of prey killed by *Coleomegilla maculata lengi* for each pest species as established in the prey utilization test divided by the corresponding Cabbage Looper Equivalency (CLE) established by Harcourt et al. (1955). CLE has been determined based on the total larval foliar consumption of each lepidopterous species. The foliar consumption of *A. rapae* and *P. xylostella* larvae were standardized according to the consumption of a *T. ni* larva (One CLE = One *T. ni*, 1.5 *A. rapae*, 5 *P. xylostella*) (Shelton et al., 1982). The CLE for *P. xylostella* was decreased to 1 CLE = 5 rather than 1 CLE = 20 as determined by Shelton et al. (1982), because it better represents its potential for qualitative damage (Dornan et al., 1994). Data were subjected to a 3-way ANOVA (SuperANOVA, Abacus Concepts, 1991) to test the influence of prey species, prey age, and predator age on the average Protection Index. When interactions between factors occurred, simple contrasts within the global model were performed.

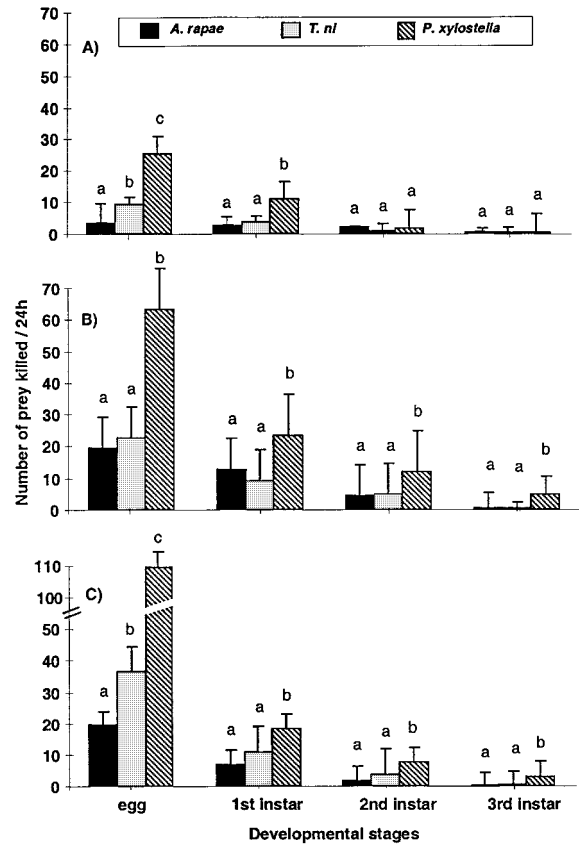


Figure 1. Predation (number of prey killed per day \pm s.e.) by (A) second instar, (B) fourth instar and, (C) adult *C. maculata* on immature instars of three lepidopterous pests. Different letters within a same prey instar indicate significant differences at $P=0.05$ by pairwise comparisons among least square means.

Results

Differential predation. All *Coleomegilla maculata lengi* stages tested successfully attacked the eggs and the first three instars of all three lepidopterous species (Figure 1). In preliminary tests, the fourth instar larvae of *T. ni* and *A. rapae* were not attacked while coccinellid larvae and adults killed, on average, less than one individual of *P. xylostella* fourth instar larvae per day. Significant interactions between the factors tested were noted ($F=2.59$; $df=12$; $P=0.0023$) indicating that the three stages of *Coleomegilla maculata lengi* differed in their predation responses depending on prey size and prey species.

Generally, utilization of all three prey species decreased with prey age ($F=477.97$ $df=3$; $P<0.0001$) (Figure 1). *Coleomegilla maculata lengi* was more efficient against eggs and first instar larvae whereas

Table 1. Comparative fresh weight (mean fresh weight [mg \pm s.d.]) of immature stages of the lepidopterous prey species and number of successful attacks by *C. maculata* (needed to obtain 1 mg in prey weight consumption)

Prey	Immature stages			
	Egg	1st instar	2nd instar	3rd instar
<i>A. rapae</i>	0.094 \pm 0.005 ^a (10.6)*	0.649 \pm 0.087 ^a (1.6)	2.238 \pm 0.346 ^b (0.48)	11.996 \pm 5.042 ^c (0.12)
<i>T. ni</i>	0.084 \pm 0.005 ^a (11.9)	0.237 \pm 0.040 ^a (4.2)	1.777 \pm 1.000 ^b (0.56)	10.450 \pm 1.801 ^c (0.12)
<i>P. xylostella</i>	0.036 \pm 0.003 ^a (27.8)	0.172 \pm 0.015 ^a (5.8)	0.466 \pm 0.104 ^a (1.6)	2.967 \pm 0.741 ^b (0.36)

Means followed by different letters within the same row are significantly different (Fisher's protected LSD test; $P < 0.05$).

*Number of successful attacks needed to obtain 1 mg in prey weight consumption.

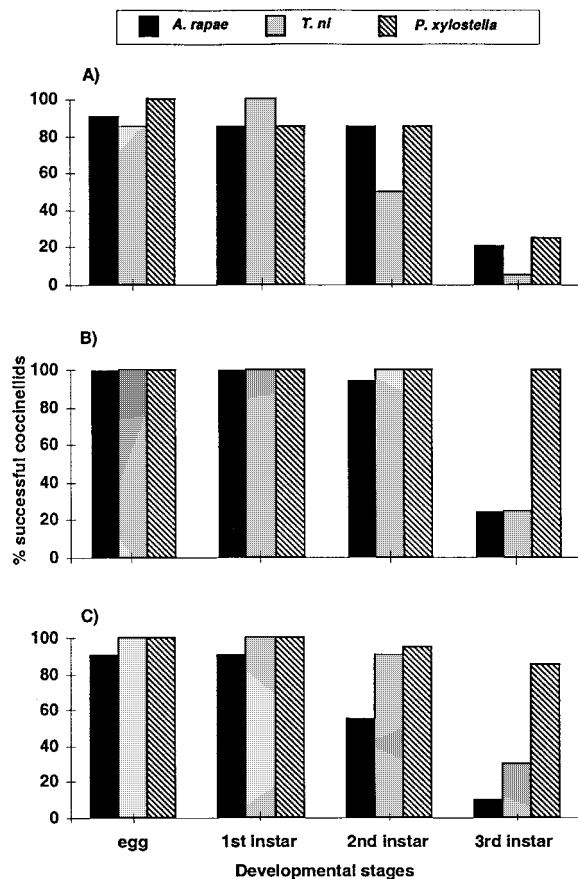


Figure 2. Percentage of (A) second instar, (B) fourth instar and, (C) adult *C. maculata* that successfully attacked at least one prey over a period of 24 h.

older prey larvae were significantly less vulnerable to predation. Furthermore, more than 85% of the predaceous coccinellids tested successfully attacked and consumed at least one egg, first or second prey instar in a 24 h period (Figure 2). However, when confronted with third instar larvae, capture efficacy significantly decreased with an average of 36% successful coccinellids ($\chi^2 = 253.74$; $df=3$; $P < 0.0001$). Within a prey instar, *Coleomegilla maculata lengi* second instar larvae were more voracious toward the eggs and first-instar larvae of *P. xylostella* compared to those of the other two prey species (*A. rapae*: $F=30.96$; $df=1$; $P < 0.0001$; *T. ni*: $F=58.79$; $df=1$; $P < 0.0001$) (Figure 1). However, they did not show any differences in their predation efficacy on second- and third-instar *P. xylostella* larvae compared to *A. rapae* and *T. ni* larvae of the same age ($P > 0.05$). Furthermore, *Coleomegilla maculata lengi* second instar larvae had a low capture efficacy on late instar prey (Figure 2). When these small predators occasionally killed larger prey, they only consumed them by partially sucking the body fluids. Overall, *Coleomegilla maculata lengi* fourth instar larvae and adults also had a higher predation rate toward immature individuals of *P. xylostella* compared to those of the two other prey species (Figure 1) but they generally killed *T. ni* and *A. rapae* immature instars in the same proportion ($P > 0.05$).

Weights of the three developmental stages of *Coleomegilla maculata lengi* differed significantly ($F=52.73$; $df=2$; $P=0.0002$). Fourth instar larvae and adults were approximately nine times larger (9.93 mg \pm 2.21) than second instar larvae (0.84 mg \pm 0.05).

Predator size (age) significantly affected the level of prey utilization ($F=43.10$; $df=2$; $P < 0.0001$). Overall, predation efficacy of second instar coccinellids

was significantly lower compared to *Coleomegilla maculata lengi* adults ($F=183.22$; $df=1$; $P<0.0001$) and fourth-instar larvae ($F=207.61$; $df=1$; $P<0.0001$) (Figure 1). However, predation rate on third instar prey was similar between all predatory coccinellid stages ($P>0.05$) even if the percentage of predators which caught prey was significantly lower for *Coleomegilla maculata lengi* second instar larvae compared to the other two predaceous instars ($\chi^2 = 25.80$; $P<0.0001$) (Figure 2). It is also interesting to notice that, when significant differences were observed in predation behaviour between *Coleomegilla maculata lengi* fourth instars and adults, the predaceous larvae always showed a higher predation rate on lepidopterous larvae ($F=207.61$; $df=1$; $P<0.0001$) whereas coccinellid adults were more efficient on eggs ($F=27.21$; $df=1$; $P<0.0001$).

Coleomegilla maculata lengi prey weight consumption. Prey weight differed significantly between prey species ($F=32.3$; $df=2$; $P<0.0001$) and age classes ($F=199.4$; $df=3$; $P<0.0001$) (Table 1). Overall, *P. xylostella* immatures had a significant lower weight (approximately 50%) than the immatures of the two other lepidopterous prey species.

To test the influence of prey body size on prey utilization by *Coleomegilla maculata lengi*, prey weight consumption rate was compared to the weight of each immature prey stage offered (Figure 3). Using data obtained with all *Coleomegilla maculata lengi* stages, it appeared that utilization of prey immatures of intermediate sizes was higher compared to small or large prey which induced a prey utilization curve that was convex to the prey weight axis ($R^2 = 0.23$; $P=0.0090$) and peaked at a prey weight of 5.5 mg. The shape of the curve varied mainly according to predator size (age). *Coleomegilla maculata lengi* second instar larvae had a low efficacy rate in utilizing prey of most sizes producing no significant convex curve ($R^2=0.041$; $P>0.05$). Fourth instar larvae and adults had significant convex prey utilization curves that peaked at a prey weight consumption rates of 12.0 and 7.2 mg day⁻¹, respectively (Figure 3).

Effect of CLE on prey utilization results. *Coleomegilla maculata lengi* had a higher predation level on *P. xylostella* eggs and larvae than on other prey (Figure 1). However, when these data are combined with a measure of foliar consumption by the three lepidopterous pest species (CLE) in order to evaluate the beneficial impact of predation by *Coleomegilla maculata lengi*

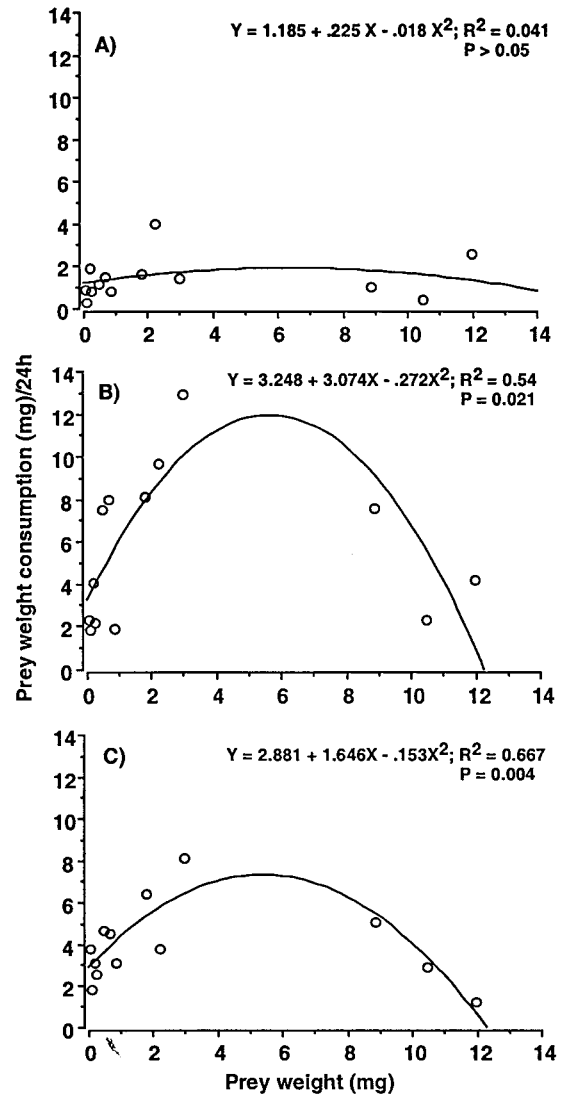


Figure 3. Prey weight consumption by (A) second instar, (B) fourth instar and, (C) adult *C. maculata* in a 24 h period in relation to the weight of each prey stage offered. Results for eggs, first-, second-, and third instar larvae are presented for *A. rapae* and *T. ni* and eggs, first-, second-, third- and fourth instar larvae are presented for *P. xylostella*. Data on immatures of all three lepidopterous species are pooled for each *C. maculata* stage.

(PI), it appeared that the highest impact of predation was on *T. ni* immatures ($F=49.72$; $df=2$; $P<0.0001$) (Figure 4). This Protection Index decreased with prey age for all prey species tested ($F=500.71$; $df=3$; $P<0.0001$). Fourth instar larvae as well as adult *Coleomegilla maculata lengi* were significantly more efficient compared to second instar larvae ($F=132.12$; $df=2$; $P<0.0001$).

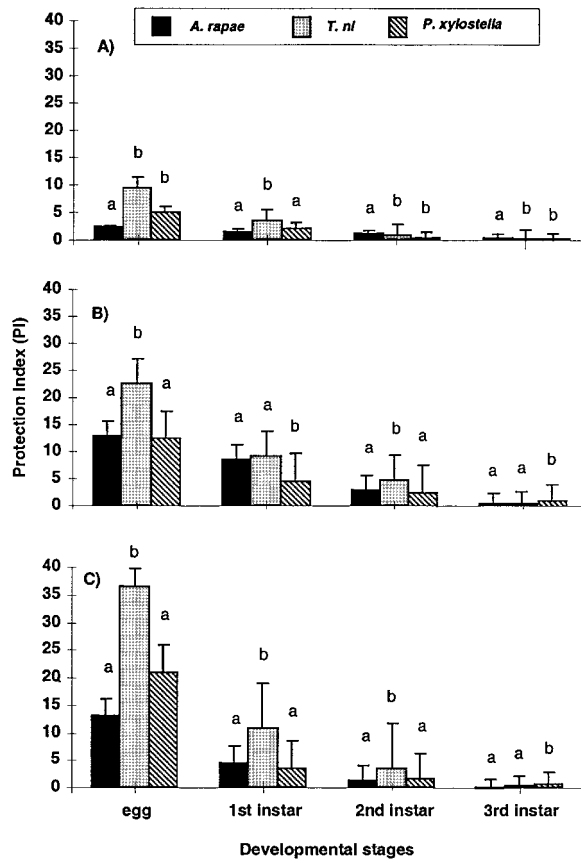


Figure 4. Protection Index (PI) \pm s.e. for (A) second instar, (B) fourth instar and, (C) adult *C. maculata lengi*. The PI is the number of prey killed divided by the corresponding Cabbage Looper Equivalency (CLE). Different letters within a same prey stage indicate significant differences at $P=0.05$ by pairwise comparisons among least square means.

Discussion

The present study demonstrates that immatures of the three lepidopterous species are acceptable prey for the generalist predator *Coleomegilla maculata lengi*. The predaceous larvae and adults consumed all prey instars except for the last instar of *T. ni* and *A. rapae*. There was an inverse relation between the number of prey killed and prey size (Figure 1) which is consistent with other laboratory studies conducted with *Coleomegilla maculata lengi* in similar laboratory conditions (Gorden et al., 1990; Giroux et al., 1995).

Even if predation rate was higher on small immatures, they are not necessarily the most suitable prey for this predator. According to optimal foraging theory, predators are expected to utilize large prey in an effort to maximize energy return (Schoener, 1969). On

the other hand, consuming smaller prey may be adaptive if large prey are costly in terms of injury risks. Hence, even if the nature of costs associated to utilization of small or large prey are different, they both could result in a lower net energy gain than intermediate sized prey. Based on these assumptions, our main prediction was that, all other factors being equal, a generalist predator like *Coleomegilla maculata lengi* should have a better prey weight consumption rate on prey of intermediate size because they represent the best trade-off in terms of predation costs and instantaneous rate of energy gain. If we assume that the rate of weight consumption is a good indication of the instantaneous rate of energy gain, the results obtained support this prediction. As expected, prey weight consumption by fourth instar larvae and adult *Coleomegilla maculata lengi* was higher on prey immatures of intermediate size leading to a convex prey weight consumption curve (Figure 3). Thus, even if *Coleomegilla maculata lengi* consumed a higher number of small prey (Figure 1), they were not of high energetic value for this predator because it had to attack and consume many small prey to obtain sufficient energy (Table 1). Results showed that they obtained more total biomass from intermediate sized prey than from either small or large prey.

The predatory behaviour of a coccinellid is mainly composed of three major components: searching, prey capture and consumption (Nakamuta, 1983). This sequence, defined as a feeding bout, has to be entirely followed for each prey encounter. Therefore, costs associated with each of the predatory components can vary and consequently influence the optimal prey utilization level. When foraging in an environment containing only small prey, a predator has to spend more time searching because of the large number of prey it has to subdue to gain sufficient energy. In this case, search time can be viewed as placing an upper limit on the prey consumption rate of small prey and this could have obvious implications for predator fitness, as there is a negative correlation between time invested in searching (and the risk associated with this activity) and net energy gain (Crawley & Krebs, 1992). Higher investment in searching time and low energetic value of small prey compared to larger prey may increase lost opportunity time on larger prey for *Coleomegilla maculata lengi*.

Coccinellid larvae usually locate prey by physical contact (Storch, 1976; Carter & Dixon, 1984) and/or by olfactory stimuli (Hodek & Honek, 1996) while adults may use olfactory stimuli and visual

contact but only at a very short distance (Stubbs, 1980; Hattingh & Samways, 1995). Because of this poor visual acuity, predaceous coccinellids must usually take the decision to attack and subdue or to give up upon encounter. Hence, for coccinellids, prey utilization is related mostly to prey availability (Carter & Dixon, 1982) and to the relative vulnerability of the food items (Wratten, 1973). Because defense responses of large prey are usually more efficient than those of smaller sized prey (Dixon, 1959; Hajek & Dahlsten, 1987), their utilization increases the probability of injury for the predators. These differences in prey vulnerability could have reduced the capture efficacy of *Coleomegilla maculata lengi* on late instars (Figure 2) and increased the time allocated to their manipulation (handling time), consequently provoking a decrease in prey weight consumption (Figure 3). Thus, despite the fact that the instantaneous energy gain per individual is higher on large prey, the time lost and the risk of injury associated with their capture and consumption could also have placed an upper limit on the prey consumption rate observed.

The complexity of the environment in which a predator forages can influence the magnitude of the costs and benefits associated with this activity. The simplified experimental system used in these experiments simulated a clumped distribution of lepidopterous prey not normally observed in the field (Harcourt, 1962). Predaceous coccinellids have a searching behaviour adapted to prey with a clumped distribution. After a prey encounter, a decrease in speed and an increase in turning rate (intensive foraging) augment the probability of locating another prey individual (Dixon, 1959; Nakamura, 1982). The artificial prey aggregation possibly reduced the searching time and resulted in a higher consumption rate than should normally be expected in a natural and more complex environment. Furthermore, in an environment where prey individuals are scattered, because of its poor visual capacities, coccinellids could overlook small prey and show lower encounter rate. Frazer et al. (1981) showed that larvae of three predaceous coccinellid species often failed to detect small aphid instars consequently increasing the time spent searching for potential prey. The simplified plant structure used here may also have reduced the potential for escape or refuge. We assume that costs involved to obtain a sufficient amount of energy are minimized in a simplified environment which favors a higher utilization rate of prey at both ends of the size spectrum. Consequently, in nature, we should expect a steeper prey weight consumption bell shape curve

with a prey consumption rate that still peaks at an intermediate prey size range.

Defense responses do not only increase with prey size (age) but can also be different between prey species (Dixon, 1958; Hajek & Dahlsten, 1987; Chow & Mackauer, 1991). The three lepidopterous species we studied have different morphology, mobility capacity and defense behaviour that can influence their level of vulnerability to natural enemies. All other aspects of prey availability and suitability being equal, these variations in the nature and effectiveness of prey aggressive behaviour might determine the outcome of prey utilization by *Coleomegilla maculata lengi*. Behavioural observations realized during the tests showed that *T. ni* and *P. xylostella* larvae exhibited an array of active defensive responses such as violent wriggling in the presence of a predator, a behaviour also observed by Harcourt (1957). These caterpillars also threw themselves off the cabbage leaf to which they remained attached by a silk thread. Whenever a coccinellid approached, *T. ni* larvae also displayed conspicuous postures to startle the coccinellid predators (projecting the front end of the body upward). When confronted to such kinds of behaviour, many coccinellids did not pursue their attack. In contrast, *A. rapae* usually stayed rather stationary and, as also observed by Ohsaki & Sato (1990), displayed virtually no active defensive behaviour. However, this relative immobility can act as a passive defense system. In fact, Hajek & Dahlsten (1987) showed that in 50% of encounters with stationary aphids, *Adalia bipunctata* larvae walked over the aphids without exhibiting intensified searching behaviour.

However, even if these lepidopterous prey exhibited different defense responses, it did not result in consistent differences in the capture efficacy of *Coleomegilla maculata lengi* between prey species. Within a prey instar, prey utilization was higher on individuals of the smallest prey species (*P. xylostella*). We suggest that this higher efficacy on *P. xylostella* was induced by differential prey size within a prey instar (Table 1) and not by differences in defense responses. For instance, *P. xylostella* third instar larvae were more utilized than *A. rapae* and *T. ni* of the same age but of different size.

The upper limit of prey size utilization is generally determined by the ability of the predator to search, capture and subdue the prey items (Malcolm, 1992). Generally, second instar *Coleomegilla maculata lengi* consumed a lower number of prey of all sizes compared to adults and fourth instar larvae (Figure 1),

a situation also observed in other coccinellid species (Dixon, 1959; Wratten, 1976; Hajek & Dahlsten, 1987). This resulted in a rather flat curve in prey weight consumption for these young and small coccinellids (Figure 3). Usually predatory arthropods tend to attack prey smaller than themselves (Sabelis, 1992). Most of the prey offered to the second instar coccinellids were of similar size or larger, whereas adults and fourth instar larvae were usually larger than the prey encountered. Hence, these differences in the size ratio were detrimental to second instar larvae not only with large prey but also with prey of intermediate size. The few encounters that we observed between young coccinellid larvae and prey larger than themselves, suggest that some attacks might result in injury or fail entirely. Furthermore, second instar coccinellids are less mobile compared to late instar larvae and adults (Wratten, 1973; Hajek & Dahlsten, 1987), and less effective in manipulating prey (Dixon, 1959) consequently reducing the prey utilization level on most prey sizes.

Even if the overall predation efficacy of adults and fourth instar *Coleomegilla maculata lengi* was similar, egg utilization was higher for adults whereas prey larvae were more vulnerable to fourth instar larvae. Dixon (1959) proposed that the lower efficiency of adults on prey larvae could be caused by the fact that adults are more conspicuous (colored with an hemispherical shape) than the coccinellid larvae. Hence, a larval prey has more warning and can react more rapidly to the approach of a coccinellid adult. Better visual acuity of coccinellid adults can explain their higher efficacy on lepidopterous eggs compared to fourth instar larvae.

Overall, our results clearly indicate that the generalist predator *Coleomegilla maculata lengi* prey differentially according to predator/prey size ratio. Because prey size is positively correlated with prey age, the age structure of the lepidopterous population in the field can be expected to influence the level of predation. The outcome of these predator-prey interactions can have a determining effect on the level of plant damage induced by the pest. The Protection Index (PI) that we developed quantifies the reduction by *Coleomegilla maculata lengi* of plant damage caused by the lepidopterous complex. We showed in this study that *Coleomegilla maculata lengi* was more efficient in utilizing *P. xylostella* immatures. However, because of the higher level of damage caused by *T. ni* larvae, the PI indicates that *Coleomegilla maculata lengi* should have a more significant beneficial impact when

it preys on *T. ni* immatures (Figure 4). Furthermore, because of their high efficacy on eggs and small lepidopterous larvae, adults or fourth instar *Coleomegilla maculata lengi* should be released early when the first lepidopterous eggs or young larvae are observed.

Predation will significantly influence the population dynamics of the prey species and the primary production of the cruciferous crops depending on (1) the predation behaviour of *Coleomegilla maculata lengi* in the presence of alternative prey, (2) the relative proportion of the lepidopterous pest complex present, (3) the influence of other natural enemies and, (4) the specific conditions of the agricultural system.

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References

- Abacus Concepts, 1991. Super ANOVA, the accessible general linear modeling package (v1.11 for the Macintosh Computer). Abacus Concepts, Inc., Berkeley, California.
- Abacus Concepts, 1994. StatView. Abacus Concepts, Inc., Berkeley, CA.
- Andow, D. A., 1990. Characterization of predation on egg masses of *Ostrinia nubilalis* (Lepidoptera: Pyralidae). *Annals of the Entomological Society of America* 83: 482–486.
- Carter, M. C. & A. F. G. Dixon, 1982. Habitat quality and the foraging behaviour of coccinellid larvae. *Journal of Animal Ecology* 51: 865–878.
- Carter, M. C. & A. F. G. Dixon, 1984. Foraging behaviour of coccinellid larvae: duration of intensive search. *Entomologia Experimentalis et Applicata* 36: 133–136.
- Charnov, E. L., 1976. Optimal foraging, the marginal value theorem. *Theoretical Population Biology* 9: 129–136.
- Chow, A. & M. Mackauer, 1991. Patterns of host selection by four species of aphidiid (Hymenoptera) parasitoids: influence of host switching. *Ecological Entomology* 16: 403–410.

- Chau, A. & M. Mackauer, 1997. Dropping of pea aphids from feeding site: a consequence of parasitism by the wasp, *Nonocotomus paulensis*. *Entomologia Experimentalis et Applicata* 83: 247–252.
- Coderre, D., L. Provencher & J. Tourneur, 1987. Oviposition and niche partitioning in aphidophagous insects on maize. *Canadian Entomologist* 119: 195–203.
- Coll, M. & D. G. Bottrell, 1991. Microhabitat and resource selection of the European corn borer (Lepidoptera: Pyralidae) and its natural enemies in Maryland field corn. *Environmental Entomology* 20: 526–533.
- Crawley, M. J. & J. R. Krebs, 1992. Foraging theory. In: M. J. Crawley (ed.), *Natural Enemies*. Blackwell Scientific Publications, Oxford, pp. 90–114.
- Dixon, A. F. G., 1958. The escape responses shown by certain aphids to the presence of the coccinellid *Adalia decempunctata* (L.). *Transactions of the Royal Entomological Society of London* 110: 319–334.
- Dixon, A. F. G., 1959. An experimental study of the searching behaviour of the predatory coccinellid beetle *Adalia decempunctata* (L.). *Journal of Animal Ecology* 28: 259–281.
- Dornan, A. P., J. G. Stewart & M. K. Sears, 1994. An action threshold for control of lepidopterous pests of cabbage in Prince Edward Island. *Canadian Entomologist* 126: 379–387.
- Frazer, B. D., N. Gilbert, P. M. Ives & D. A. Raworth, 1981. Predation of aphids by coccinellid larvae. *Canadian Entomologist* 113: 1043–1046.
- Giroux, S., R. M. Duchesne & D. Coderre, 1995. Predation of *Leptinotarsa decemlineata* (Coleoptera: Chrysomelidae) by *Coleomegilla maculata* (Coleoptera: Coccinellidae): comparative effectiveness of predator developmental stages and effect of temperature. *Environmental Entomology* 24: 748–754.
- Groden, E., F. A. Drummond, R. A. Casagrande & D. L. Haynes, 1990. *Coleomegilla maculata* (Coleoptera: Coccinellidae): Its predation upon the Colorado potato beetle (Coleoptera: Chrysomelidae) and its incidence in potatoes and surrounding crops. *Journal of Economic Entomology* 83: 1306–1315.
- Hajek, A. E. & D. L. Dahlsten, 1987. Behavioral interactions between three birch aphid species and *Adalia bipunctata* larvae. *Entomologia Experimentalis et Applicata* 45: 81–87.
- Harcourt, D. G., 1957. Biology of the diamondback moth, *Plutella maculipennis* (Curt.) (Lepidoptera: Plutellidae), in eastern Ontario. II. Life-history, behaviour, and host relationships. *Canadian Entomologist* 89: 554–564.
- Harcourt, D. G., 1962. Biology of cabbage caterpillars in eastern Ontario. *Proceedings of the Entomological Society of Ontario* 93: 61–75.
- Harcourt, D. G., R. H. Backs & L. M. Cass, 1955. Abundance and relative importance of caterpillars attacking cabbage in eastern Ontario. *Canadian Entomologist* 87: 400–406.
- Hattingh, V. & M. J. Samways, 1995. Visual and olfactory location of biotopes, prey patches, and individual prey by the ladybeetle *Chilocorus nigritus*. *Entomologia Experimentalis et Applicata* 75: 87–98.
- Hodek, I., 1993. Habitat and food specificity in aphidophagous predators. *Biocontrol Science and Technology* 3: 91–100.
- Hodek, I. & A. Honek, 1996. *Ecology of Coccinellidae*. Kluwer Academic Publishers, Dordrecht, 464 pp.
- Hodek, I., Z. Ruzika & M. Hodkova, 1978. Feeding on pollen and aphids by *Coleomegilla maculata lengi*. *Annales de Zoologie Ecologie Animale* 10: 453–459.
- Krebs, J. R. & R. H. McCleery, 1984. Optimization in behavioural ecology. In: J. R. Krebs & N. B. Davies (eds), *Behavioral Ecology, an Evolutionary Approach*, 2nd ed., Blackwell Scientific, Oxford, pp. 91–121.
- Lambin, M., A. Ferran & K. Maugan, 1996. La prise d'informations visuelles chez la coccinelle *Harmonia axyridis*. *Entomologia Experimentalis et Applicata* 79: 121–130.
- Lucas, E., D. Coderre & C. Vincent, 1997. Voracity and feeding preferences of two aphidophagous coccinellids on *Aphis citricola* and *Tetranychus urticae*. *Entomologia Experimentalis et Applicata* 85: 151–159.
- Mack, T.P. & Z. Smilowitz, 1980. Development of a green peach aphid natural enemy sampling procedure. *Environmental Entomology* 9: 440–445.
- Malcolm, S.B., 1992. Prey defence and predator foraging. In: M.J. Crawley (ed), *Natural Enemies*. Blackwell Scientific Publications, Oxford, pp. 458–475.
- Meredia, K.M., S.H. Gage, D.A. Landis & T.M. Wirth, 1992. Visual response of *Coccinella septempunctata* (L.), *Hippodamia parenthesis* (Say), (Coleoptera: Coccinellidae), and *Chrysoperla carnea* (Stephens), (Neuroptera: Chrysopidae) to colors. *Biological Control* 2: 253–256.
- Mills, N. J., 1981. Essential and alternative foods for some British Coccinellidae (Coleoptera). *Entomologist's Gazette* 32: 197–202.
- Nakamura, K., 1982. Switchover in searching behavior of *Coccinella septempunctata* L. (Coleoptera: Coccinellidae) caused by prey consumption. *Applied Entomology and Zoology* 17: 501–506.
- Nakamura, K., 1983. Sequence of predatory behavior of the ladybeetle, *Coccinella septempunctata* L. (Coleoptera: Coccinellidae) on the green peach aphid, *Myzus persicae* Sulzer (Homoptera: Aphididae). *Applied Entomology and Zoology* 18: 558–561.
- Obrycki, J.J. & C.J. Orr, 1990. Suitability of three species of aphids for Nearctic populations of *Coccinella septempunctata*, *Hippodamia variegata*, and *Propylea quatuordecimpunctata* (Coleoptera: Coccinellidae). *Journal of Economic Entomology* 83: 1292–1297.
- Ohsaki, N. & Y. Sato, 1990. Avoidance mechanisms of three *Pieris* butterfly species against the parasitoid wasp *Apanteles glomeratus*. *Ecological Entomology* 15: 169–176.
- Pastorok, R.A., 1981. Prey vulnerability and size selection by *Chaoborus* larvae. *Ecology* 62: 1311–1324.
- Pimentel, D., 1961a. Natural control of aphid populations on cole crops. *Journal of Economic Entomology* 54: 885–888.
- Pimentel, D., 1961b. Natural control of caterpillars populations on cole crops. *Journal of Economic Entomology* 54: 889–892.
- Richards, O.W., 1940. The biology of the small white butterfly (*Pieris rapae*), with special reference to the factors controlling its abundance. *Journal of Animal Ecology* 9: 243–288.
- Roger, C., G. Boivin & D. Coderre, 1995. Potentiel de la coccinelle maculée comme agent de lutte biologique contre les lépidoptères ravageurs des crucifères. *Research Summary. Horticultural Research & Development Centre, St-Jean-sur-Richelieu/L'Assomption* 24: 23–24.
- Sabelis, M. W., 1992. Predatory arthropods. In: M. J. Crawley (ed), *Natural Enemies*. Blackwell Scientific Publications, Oxford, pp. 225–264.
- Schoener, T. W., 1969. Models of optimal size for solitary predators. *American Naturalist* 103: 277–313.
- Shelton, A. M., J. T. Andaloro & J. Barnard, 1982. Effects of cabbage looper, imported cabbageworm, and diamondback moth on fresh market and processing cabbage. *Journal of Economic Entomology* 75: 742–745.

- Shelton, A. M., R. J. Kroening, M. K. Wilsey & S. D. Eigenbrode, 1991. Comparative analysis of two rearing procedures for diamondback moth (Lepidoptera: Plutellidae). *Journal of Entomological Science* 26: 17–26.
- Smith, B. C., 1960. A technique for rearing coccinellid beetles on dry foods, and influence of various pollens on the development of *Coleomegilla maculata lengi* Timb. (Coleoptera: Coccinellidae). *Canadian Journal of Zoology* 38: 1047–1049.
- Stephens, D. W. & J. R. Krebs, 1986. *Foraging Theory*. Princeton University Press, Princeton.
- Storch, R. H., 1976. Prey detection by fourth stage *Coccinella transversoguttata* larvae (Coleoptera: Coccinellidae). *Animal Behaviour* 24: 690–693.
- Stubbs, M., 1980. Another look at prey detection by coccinellids. *Ecological Entomology* 5: 179–182.
- Webb, S. E. & A. M. Shelton, 1988. Laboratory rearing of the imported cabbageworm. *New York Food and Life Sciences Bulletin* 122, 6pp.
- Wratten, S. D., 1973. The effectiveness of the coccinellid beetle, *Adalia bipunctata* (L.), as a predator of the lime aphid, *Eucalipterus tiliae* L. *Journal of Animal Ecology* 42: 785–792.
- Wratten, S. D., 1976. Searching by *Adalia bipunctata* (L.) (Coleoptera: Coccinellidae) and escape behaviour of its aphids and cicadellid prey on lime (*Tilia vulgaris* Hayne). *Ecological Entomology* 1: 139–142.