

Predation upon the oblique-banded leafroller, *Choristoneura rosaceana* (Lepidoptera: Tortricidae), by two aphidophagous coccinellids (Coleoptera: Coccinellidae) in the presence and absence of aphids

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Abstract. Our goal has been to determine the effect of the presence of aphids on voracity (measured as number of prey eaten and biomass consumed) of *Coccinella septempunctata* L. and *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) feeding upon the oblique-banded leafroller, *Choristoneura rosaceana* (Harris) (Lepidoptera: Tortricidae). For each coccinellid predator, treatments using a single prey species, with either 30 first instar *C. rosaceana* or 100 third instars *Aphis pomi* DeGeer (Hemiptera: Aphididae), were compared with two-prey treatments in which the two prey species were present simultaneously. For both predators, the total number of prey killed (total prey species pooled) and the total biomass consumed were significantly higher when both prey were present than in single-prey treatments. The voracity of *C. septempunctata* on *C. rosaceana* larvae was not affected by adding *A. pomi*, whereas that of *H. axyridis* declined; the voracity of both predators on *A. pomi* increased when *C. rosaceana* larvae were added. The preference for the aphids over *C. rosaceana* was confirmed for both coccinellid species.

INTRODUCTION

The oblique-banded leafroller, *Choristoneura rosaceana* (Harris) (Lepidoptera: Tortricidae), feeds on a wide range of plant species including rose (*Rosa* spp.), dewberry (*Rubus flagellaris* L.), raspberry (*Rubus idaeus* L.), blueberry (*Vaccinium corymbosum* L.), apple (*Malus domestica* Borkh.), peach (*Prunus persica* Botsch), pear (*Pyrus communis* L.), cherry (*Prunus avium* L.), European hazel (*Corylus avellana* L.), pistachio (*Pistacia vera* L.), and forest trees (Chapman & Lienk, 1971). In apple orchards, outbreaks have become more severe during the last 10–15 years in the United States and Canada, as *C. rosaceana* can damage apple trees seriously by attacking floral parts, fruit and leaves (Reissig, 1978). *C. rosaceana* became resistant to several insecticides registered in the USA (Reissig, 1978; Reissig et al., 1986) and Canada (Carrière et al., 1994; Smirle et al., 1998; Pree et al., 2001), necessitating the investigation of biological control methods that have radically different modes of action.

Among the aphidophagous coccinellid (Coleoptera: Coccinellidae) species found in orchards of eastern Canada (Tourneur et al., 1992), the seven spotted ladybeetle, *Coccinella septempunctata* L., and the asiatic ladybeetle, *Harmonia axyridis* Pallas, are the most common. They constitute potential biocontrol agents, owing to their ubiquity and competitive abilities. *C. septempunctata* is a voracious predator that can attack ca. 100 prey species including aphids, psyllids, coccids, thrips, leaf

beetles and lepidopteran larvae (Iablokoff-Khnzorian, 1982; Kring et al., 1985; Kareiva, 1987; Horn, 1991). It is abundant in apple orchards of North America, including Michigan (Maredia et al., 1992) and Quebec (Tourneur et al., 1992). *H. axyridis* has been introduced to the United States (Chapin & Brou, 1991; Tedders & Schaefer, 1994) and became established in Canada in 1994 (Coderre et al., 1995). In Europe, *H. axyridis* is used to control aphid populations in orchards (Ongagna et al., 1993). *H. axyridis* is reported to be one of the most polyphagous coccinellid species (Hodek, 1996; Lucas et al., 1997, 1998b).

Both coccinellid species have been reported to attack lepidopteran prey (Iablokoff-Khnzorian, 1982; Horn, 1991; Mohan et al., 1991) and may have potential as natural enemies of the oblique-banded leafroller. However, both species belong to the aphidophagous coccinellid group and prey mainly on aphids. Predators may respond to the presence of a second prey species in different ways: 1) they may have a strong preference for one prey species and concentrate their efforts on this prey even when both prey are present or, 2) they may have no preference and attack any prey of whatever species is encountered or, 3) they may concentrate their attacks on the commonest prey and switch from one prey to another according to their respective densities (Murdoch & Marks, 1973). The type of response may determine the potential efficiency of any biological control program because the presence of aphids may affect the predation efficacy of the ladybeetles against the leafroller.

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The apple aphid, *Aphis pomi* DeGeer (Hemiptera: Aphididae), is a major pest in most commercial orchards and some of its populations have become resistant to a number of insecticides in the USA (Carroll & Hoyt, 1984). Under favorable conditions, and due to its parthenogenic development (Dixon, 1985), the populations quickly can exceed economic thresholds and cause serious damage (Carroll & Hoyt, 1984). *A. pomi* is preyed upon by both *C. septempunctata* (Iablokoff-Khnzorian, 1982) and *H. axyridis* (Hukusima & Kamei, 1970) and is encountered in apple orchards at the same time as *C. rosaceana*. Both *A. pomi* and *C. rosaceana* are also encountered at the same time in the field during July and August in Quebec (Chouinard et al., 2000).

Our objective was to determine how the presence of the apple aphid affects the predation efficacy of *C. septempunctata* and *H. axyridis* on the obliquebanded leafroller. The voracity of both predators was evaluated using first instar *C. rosaceana* in the presence and absence of third instar *A. pomi*. Owing to their aphidophagous habits, it was expected that predation on the leafroller might be reduced in the presence of aphids.

MATERIALS AND METHODS

Insects. Overwintered *Choristoneura rosaceana* larvae were collected in a commercial apple orchard at Saint-Joseph-du-Lac (73°53'01"W; 45°31'58"N), Quebec, Canada. They were reared on an artificial diet of pinto beans (Shorey & Hale, 1965). The aphids were collected periodically from a *Cotoneaster acutifolius* (Hort.) hedge in Montreal (73°39'W; 45°30'N), Quebec. Third instar *Aphis pomi* were selected for the experiments. *Coccinella septempunctata* adults were collected in strawberry (*Fragaria x ananassa* Duch.) fields in the Saint-Jean-sur-Richelieu (73°15'00"W; 45°18'58"N) area (Quebec, Canada). A population of *Harmonia axyridis* of Chinese origin was reared on *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) eggs. Both predators were reared for at least two weeks on a diet composed of several species of aphids (mainly *Aphis citricola*, excluding *A. pomi*), a 20% sucrose solution and wild flower pollen. They were starved 24 h before the experiments.

Experimental design. The experiment was done at 23°C (± 1°C), 16L : 8D, and 60% RH. The experimental setup consisted of two 15-cm-diameter plastic pots fitted one within the other (Lucas et al., 1997). The upper pot (8 cm high) contained an apple tree sapling (*Malus domestica* Borkhausen; cultivar Empire; 5–7 weeks old; five leaves), whose roots were soaked in water contained in the lower pot (15 cm high). The prey and the predators were deposited on the leaves and were allowed to settle for 15 minutes. They were observed through a plastic film enclosing the upper pot.

Each species of predator (*C. septempunctata* and *H. axyridis* unsexed adults) was subjected to the following treatments: 1) 30 first instar *C. rosaceana* ("leafroller treatment"), 2) 100 third instar *A. pomi* ("aphid treatment"), or 3) 30 first instar *C. rosaceana* and 100 third instar *A. pomi* ("two-prey treatment"). Such densities are frequently observed in field situations (C. Vincent pers. com.). Preliminary tests showed that the number of prey offered substantially exceeded the number of prey that the predators could eat daily. Thirty replicates of each treatment and 30 of control treatments (no predators) were carried out. After 24 h the voracity of the predators was assessed as the number and biomass of preys consumed.

Data analysis. The number of prey consumed was corrected by subtracting the mean mortality in the controls from the mortality observed in each of the experimental setups containing a predator. To estimate the ingested biomass, the mean weights of first instar *C. rosaceana* (0.498 mg; n = 50) and of third instar *A. pomi* (0.147 mg; n = 200) were determined; first instar *C. rosaceana* eaten were approximately three times heavier than *A. pomi* nymphs. The overall predator voracity (both prey species pooled) was compared using a two-way analysis of variance (ANOVA; factors: predator and prey treatments) performed with SuperANOVA® (Abacus Concepts, 1989) and followed, when appropriate, by Fisher's Protected LSD tests. The overall number of prey eaten and the overall biomass consumed were analyzed.

To evaluate the effect of the presence of a second prey species, the number of individuals of *A. pomi* eaten and the biomass consumed, when one or two prey species were present, were compared using a two-way ANOVA. The number of individuals of *C. rosaceana* eaten and the biomass consumed were evaluated similarly for *A. pomi*.

RESULTS

Overall predator voracity (both prey species pooled). *H. axyridis* was more voracious than *C. septempunctata* ($F_{1,160} = 26.4, p < 0.0001$), eating a total of 40.8 (± 3.4; mean ± SE) and 27.3 (± 3.0) prey in 24 h, respectively. The biomass consumed by *H. axyridis* (8.64 mg) in 24 h was also significantly greater than the biomass consumed by *C. septempunctata* (5.22 mg) ($F_{1,164} = 53.4, p < 0.0001$). The interaction term (prey × predator) of the two-way ANOVAs was significant for both the number of prey eaten ($F_2 = 6.0, p = 0.0032$) and the biomass consumed ($F_2 = 10.3, p < 0.0001$). Each predator species was analyzed separately using a one-way ANOVA.

With all prey species pooled, *C. septempunctata* ate significantly more individuals when both prey were present than when only one species was available ($F_{2,81} = 67.9, p < 0.0001$) (Fig. 1A). Similar results were obtained with *H. axyridis* ($F_{2,79} = 242.7, p < 0.0001$). Both predators ate significantly more *A. pomi* than *C. rosaceana* in the single-prey treatments (*C. septempunctata*: (LSD, $p < 0.0002$); *H. axyridis*: (LSD, $p < 0.0017$). The total biomass consumed by *C. septempunctata*, 10.1 mg (prey species pooled), was also significantly greater in two-choice than in single-prey treatments ($F_{2,81} = 62.5, p < 0.0001$) (Fig. 1B). *H. axyridis* exhibited the same response, consuming an average of 14.0 mg in two-prey treatments ($F_{2,79} = 112.1, p < 0.0001$). In the single-prey treatments, the biomass of *A. pomi* and *C. rosaceana* consumed by *C. septempunctata* was similar (LSD, $p < 0.1620$), although *H. axyridis* ate more *C. rosaceana* than aphids (LSD, $p < 0.0001$).

Prey-specific predator voracity. *H. axyridis* was more voracious than *C. septempunctata* on *A. pomi* ($F_{1,105} = 11.7, p = 0.0009$), eating respectively, 49.5 (± 3.5) and 37.1 (± 3.4) individuals in 24 h. The same results were observed for *C. rosaceana* ($F_{1,112} = 58.1, p < 0.0001$), *H. axyridis* eating 10.9 (± 0.8) and *C. septempunctata* 4.9 (± 0.5) individuals. Because the interaction term of the two-way ANOVA (prey × predator) was significant when analyzing predation on *A. pomi* ($F_1 = 6.6, p = 0.0116$)

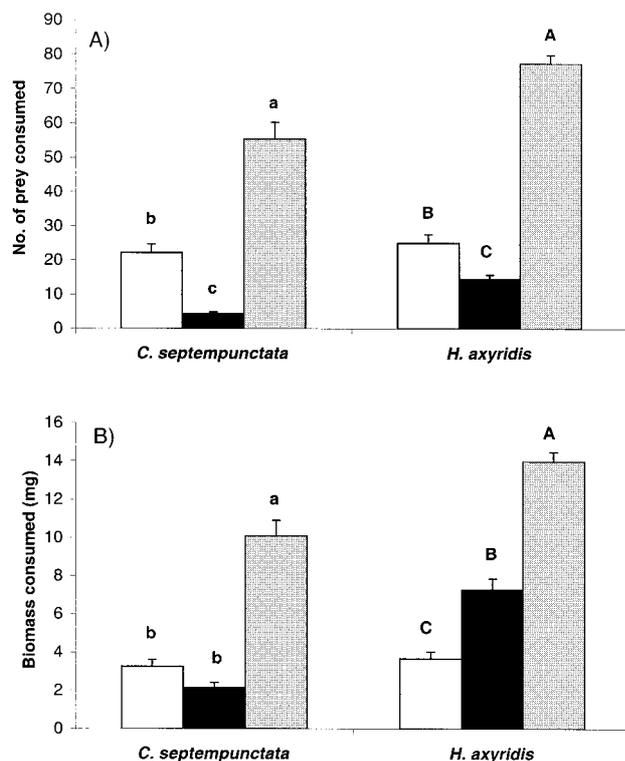


Fig. 1. Overall predator voracity (Mean + SE), by *Coccinella septempunctata* and *Harmonia axyridis* in 24 h, when offered *Aphis pomi* (white bars), *Choristoneura rosaceana* (black bars) or both prey species (grey bars). A – total number of prey predated; B – total biomass consumed. Different letters indicate a significant ($p < 0.05$) difference among the different treatments for the same coccinellid species.

and on *C. rosaceana* ($F_1 = 27.1$, $p < 0.0001$), predator treatments (species) were analyzed separately using one-way ANOVA.

In two-prey treatments, *C. septempunctata* ate significantly more *A. pomi* than in single-prey treatments ($F_{1,52} = 24.0$, $p < 0.0001$) (Fig. 2A). *H. axyridis* also ate more aphids in the presence of a second prey species ($F_{1,53} = 153.8$, $p < 0.0001$). In contrast, the voracity of *C. septempunctata* on *C. rosaceana* did not increase when aphids were present ($F_{1,57} = 2.1$, $p = 0.1493$), although the voracity of *H. axyridis* decreased significantly in the presence of aphids ($F_{1,55} = 27.3$, $p < 0.0001$). Similar results were observed for the biomass eaten (Fig. 2B).

DISCUSSION

Our experiments support three main conclusions. First, the overall voracity (prey pooled) of both predators increased when the two prey species were present. This result may be attributed to a functional response effect (Holling, 1966). An interesting question to test would be whether the simultaneous presence of both prey species also generates a numerical response effect, both reproductive and aggregative. Such an effect may increase the overall impact of predators on pest populations.

Second, both coccinellids showed a feeding preference for the aphid over the lepidopteran larva. In the two-prey treatments, *C. septempunctata* and *H. axyridis* ate both *C.*

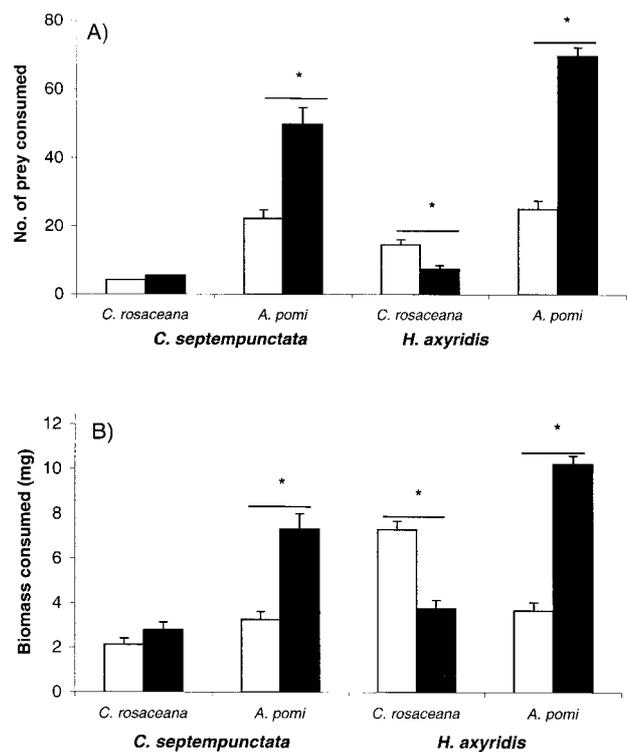


Fig. 2. Prey-specific predator voracity (Mean + SE), of *Coccinella septempunctata* and *Harmonia axyridis* in 24 h for *Choristoneura rosaceana* and *Aphis pomi*, when offered one (white bars) or two (black bars) prey species. A – number of prey predated; B – biomass consumed. Asterisks indicate a significant ($p < 0.05$) difference the single and the two-prey treatments.

rosaceana and *A. pomi*. However, they ate at least twice as many *A. pomi* than *C. rosaceana* in terms of both numbers of individuals and biomass consumed. In a previous study, *C. septempunctata* and *H. axyridis* also displayed a significant preference for the aphid *A. citricola* over the spider mite *T. urticae* at three different prey-ratios (Lucas et al., 1997). Mohan et al. (1991) also showed that *C. septempunctata* had a similar feeding preference for the aphid *Rhopalosiphum maidis* Fitch compared with *Chilo partellus* Swinhoe (Lepidoptera: Pyralidae) larvae. In 6 h, predation of *C. partellus* by *C. septempunctata* decreased significantly when both prey species were present, whereas predation of *R. maidis* remained constant whether *C. partellus* were present or not (Mohan et al., 1991). Our results confirm the preference for aphids as prey for both coccinellid species.

Third, the addition of a second prey in the system had contrasting consequences on aphids and lepidopteran larvae. For *C. rosaceana*, the addition of aphids to the system did not significantly increase the number of individuals eaten and the biomass of Lepidoptera consumed by *C. septempunctata*. However, the predation of *C. rosaceana* by *H. axyridis* decreased significantly in the presence of aphids. These results confirmed the feeding preference of both predators for aphids and showed clearly the limitations upon the efficacy of both coccinellids against lepidopteran larvae.

In contrast, the number of individuals eaten and the biomass of aphids consumed increased consistently when the second prey species was present. For the aphid, despite the fact that the second prey species differed from the first, the voracity of both predators increased as a functional response effect (Holling, 1966), meaning that the presence of an alternative (non-preferred) prey with a preferred one may generate a functional response effect toward the preferred prey, but not toward the alternative one.

It is difficult to predict what may occur in the field when both (or more) prey species are present at the same time. The outcome will depend on factors such as the priority of establishment, the spatial distribution of both prey (at plant and micro-habitat level), the presence of a third (or further) prey species, the relative densities of the different species, the feeding preferences of other predators. Our results suggest that apparent competition should be expected. Apparent competition is an indirect effect which occurs when two prey species share a common predator. An increase in the population of the first prey species, generates an increase in the predator population, causing a subsequent decrease in the population of the second prey species (Holt & Lawton, 1994; Wootton, 1994). Adding lepidopteran larvae may increase *H. axyridis* (but not *C. septempunctata*) pressure on aphids (both through numerical and functional responses). In contrast, adding aphids may decrease the predation pressure (by both predators) on lepidopteran larvae. However, we should be cautious in such a conclusion because a great number of other prey species have been identified as pests of apple orchards in North America (Oatman et al., 1964; Vincent & Bostanian, 1988; Chouinard et al., 2000). A great number of predator species attack aphids and other pests (for example more than 10 coccinellid species are found in Quebec apple orchards) and may complicate the situation (Tourneur et al., 1992).

The number of aphids consumed is probably overestimated by our experiments because, in general, many individuals leave the host plant when attacked by a predator. Minorette & Weisser (2000) observed that when *C. septempunctata* attacked a colony of 30 *Acyrtosiphon pisum* aphids, about 45% of the prey left and 45% stayed on the plant. Lucas et al. (2002) observed that, after 24 h, 18% of the *Aphis citricola* individuals (100 individuals) had left the apple sapling in the presence of *H. axyridis* and 19% in the presence of *C. septempunctata*. This could mean that the proportion of preferred/non-preferred prey might change very rapidly on a crop plant. Accordingly, the predator may switch to a non-preferred prey present on the plant or decide to leave. This fact might influence predator efficacy against the leafroller, likely by decreasing its consumption. Moreover, it was observed that *C. septempunctata* visited an aphid colony of 30 aphids for a short time (on average 80 min.) (Minorette & Weisser, 2000).

Our results and those of previous studies (Lucas et al., 1997, 1998b, 2002) confirm the higher voracity and efficacy of *H. axyridis* over *C. septempunctata* as a predator

of pests in apple orchards. Before consideration of *H. axyridis* as a sound biocontrol agent, however, the impact of the establishment of this coccinellid in Canadian apple orchards must be examined thoroughly because *H. axyridis* may affect pest populations directly by predation and indirectly by interacting with local coccinellids and other aphidophagous species via competition and intra-guild predation (Evans, 1991; Hironori & Katsuhiko, 1997; Lucas et al., 1998a, 2002).

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