

Prey Selection by the Lady Beetle *Harmonia axyridis*: The Influence of Prey Mobility and Prey Species

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*The influence of prey mobility and species on prey selection by the coccinellid *Harmonia axyridis* Pallas was determined under laboratory conditions for two prey species, *Hyaliodes vitripennis* (Say) and *Tetranychus urticae* Koch. Prey selection was influenced by prey mobility. In the presence of active prey, the coccinellid selected *T. urticae* while in presence of immobilized prey, *H. vitripennis* was preferred. *Harmonia axyridis* searching time was longer in the presence of active *H. vitripennis* than in the presence of active *T. urticae*. Moreover, the coccinellid capture rate was lower for active *H. vitripennis* caused by effective defensive mechanisms. Prey suitability was affected by prey mobility and species. Immobilized *H. vitripennis* were the most profitable prey, i.e. induced a shorter developmental time and no mortality. However, active *H. vitripennis* were not a suitable food source for *H. axyridis*. Our results suggested that three factors are involved in prey selection by *H. axyridis*: (i) prey mobility; (ii) prey defensive mechanisms; and (iii) prey species.*

KEY WORDS: foraging behavior; prey selection; prey mobility; defensive mechanisms; intraguild predation.

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INTRODUCTION

Generalist predators attack a variety of prey species that possess different energetic values, morphological characteristics and defensive mechanisms. Several energetic costs and risks are associated with prey capture. The optimal foraging theory assumes that predators select prey in order to maximize their fitness through optimal choices based on the caloric and nutritive value of prey and associated foraging costs (Stephen and Krebs, 1986). Several factors affect prey selection: (1) prey features such as species (Molles and Pietruszka, 1987; Eubanks and Denno, 2000; Roger *et al.*, 2000) size (Allan *et al.*, 1987; Molles and Pietruszka, 1987; Roger *et al.*, 2000), mobility (Clements and Harmsen, 1990; Nordlund and Morrison, 1990; Eubanks and Denno, 2000), nutritional quality (Houck, 1991; Eubanks and Denno, 2000), and population density (Jeschke and Tollrian, 2000) and (2) predator characteristics such as size (Allan *et al.*, 1987; Erickson and Morse, 1997), age (Sullivan, 1984; Cisneros and Rosenheim, 1997) and starvation (Carter and Dixon, 1982; Molles and Pietruszka, 1987; Hazzard and Ferro, 1991; Houck, 1991). Moreover, when predation occurs between two predators, several costs may be associated with the attack: higher risk of injuries, longer handling time, and high probability of unsuccessful attack (Schmidt *et al.*, 1998). Nevertheless, that type of predation is commonly observed in nature (see Polis *et al.*, 1989).

Harmonia axyridis Pallas (Coleoptera: Coccinellidae) is a generalist predator, mainly aphidophagous, but also feeding on Tetranychidae (Lucas *et al.*, 1997; Villanueva *et al.*, 2004), Psyllidae (Michaud, 2002), Curculionidae (Stuart *et al.*, 2002) and Lepidopteran species (Koch, 2003). Several studies have demonstrated that *H. axyridis* could be involved in interactions with other predators like coccinellids (Yasuda and Shinya, 1997; Cottrell and Yeorgan, 1998; Yasuda and Ohnuma, 1999; Kajita *et al.*, 2000; Burgio *et al.*, 2002; Snyder and Ives, 2004), mirids (Provost *et al.*, 2005) and lacewings (Phoofolo and Obrycki, 1998). *Harmonia axyridis* generally wins confrontations with other predators, due to its larger size and greater aggressiveness and voracity.

Hyaliodes vitripennis (Say) (Heteroptera: Miridae) is a generalist mirid predator (Arnoldi *et al.*, 1992). *Harmonia axyridis* and *H. vitripennis* are both present in Eastern Canada apple orchards where they feed on phytophagous mites, i.e. both belong to the acarophagous guild (Chouinard *et al.*, 2000). Previous studies have demonstrated that *H. axyridis* generally wins confrontation with *H. vitripennis*, but that older nymphal stages of the mirid attack vulnerable stages of the coccinellid (eggs, pupae and larva 2) (Provost *et al.*, 2005).

Prey mobility and prey species may be important factors influencing prey selection. Several studies have demonstrated that prey mobility increases searching and handling time and results in a reduced net energetic gain (e.g., Allan *et al.*, 1987; Nordlund and Morrison, 1990). However, Rosenheim and Corbett (2003) have demonstrated that for a sit-and-wait predator, high prey mobility could increase encounter rate and attack probability. Prey size could also influence prey selection. In some case, a larger prey item could supply higher nutrients but attack and capture could be more expensive and risky. Therefore, natural selection should have favoured a trade-off (Allan *et al.*, 1987; Molles and Pietruszka, 1987; Roger *et al.*, 2000).

The objective of this study was to determine the impact of prey size, prey type (intraguild or extraguild prey), and prey mobility on *H. axyridis* prey selection. We hypothesized that *H. axyridis* prey selection is affected by prey mobility, size and type. We predicted that *H. vitripennis* should be selected over *T. urticae* when *H. axyridis* foraged in the presence of immobilized prey, because the mirid has a larger size and could provide higher nutritional gain. However, in the presence of active prey, *H. axyridis* should select *T. urticae* because the efficient escape mechanisms and greater vigour of the mirid should reduce the coccinellid net energetic gain.

MATERIALS AND METHODS

Biological Material

Harmonia axyridis was collected from hibernation sites in May in the Rougemont region (45°26' N, 73°03' W) Quebec, Canada, and reared in the laboratory on *Ephesia kuehniella* Zeller. *Hyaliodes vitripennis* was collected in June in a commercial apple orchard in Rougemont and maintained in the laboratory 1–2 d on *T. urticae*. *Tetranychus urticae* was maintained in the laboratory on lima bean plants, *Phaseolus lunatus* L.. Rearing conditions were 20 ± 1°C, 60–70% RH and 16L: 8D. Before each test, *H. axyridis* were starved individually in a Petri dish for a period of 16 h (24° ± 1°C, 60–70% RH, photoperiod of 8L:8D), in order to increase their motivation to forage. Prey selection experiments were done on an apple leaf, while prey suitability experiments were conducted on vertical apple shoots, with three terminal leaves. Each shoot was placed in a 4L plastic box. Shoots and leaves were collected from apple trees in the same orchard and washed before the beginning of the experiment in order to eliminate other arthropods and pesticide residues. Experiments were conducted at 20° ± 1°C, 60–70% RH and 16L: 8D.

Prey Selection

Experiments were conducted with *H. axyridis* third instar larvae (L3) and two prey species: (1) *H. vitripennis* fourth-stage nymphs (N4), and (2) *T. urticae* adults. The specific developmental stages of *H. axyridis* and *H. vitripennis* were selected according to previous intraguild predation experiments (Provost *et al.*, 2005); because we observed similar levels of intraguild predation between *H. axyridis* and *H. vitripennis* whatever the life stages in presence, we selected those having the higher probability of encounter in natural conditions. Intraguild predation of the mirid N4 on young larva of the coccinellid was also observed so the risk of injuries and foraging costs could be important to the coccinellid for this predation combination. To determine the impact of prey mobility on prey selection, observations were done on active and immobilized prey. Immobilized prey was frozen 12 h before tests. Preliminary tests showed that frozen individuals of these two prey species were readily accepted by *H. axyridis*. Other studies also demonstrated that frozen prey were suitable to *H. axyridis* (Kalaskar and Evans, 2001).

Hyaliodes vitripennis (size of one individual = 3.0 mm) is more mobile and approximately 7.5 times larger than *T. urticae* (size of one individual = 0.4 mm). The proportion of each prey on apple leaves was 1/3 *H. vitripennis* (3 individuals) and 2/3 *T. urticae* (6 individuals). This proportion was used as a simulation of natural situations commonly encountered in July in Québec apple orchards harboring populations of both species (Chouinard, unpublished data). Visual observations of prey selection were done for a sequence of three prey consumed consecutively. Prey densities were kept constant by replacing consumed prey after each attack by adding another prey manually. The attack frequency (or percentage) was recorded for each predation event in the sequence. Fifteen replicates were carried out for each treatment.

In order to evaluate *H. axyridis* prey selection, the attack frequency on each prey between each predation event was compared to a theoretical index of (33% for *H. vitripennis* and 67% for *T. urticae*) using a conformity test (SAS Institute, 2000). The theoretical index values were established according to the respective densities of both prey.

Components of Predation

This experiment was done in order to determine which prey characteristics affect *H. axyridis* (L3) prey selection. Experiments were conducted in the presence of *H. vitripennis* (N4) and *T. urticae* (adult), both either active

or immobilized. For each observation, one *H. axyridis* larva was introduced on an apple leaf along with two prey individuals. Three parameters of the feeding behaviour of *H. axyridis* were observed:

- searching time: time between the beginning of the test and the first encounter with the prey
- capture rate: proportion of attacks ending in prey capture * 100
- handling time: time spent by *H. axyridis* to consume the prey (until the predator released the prey or finished consuming the prey).

The defensive mechanisms of active prey were also observed and classified as:

- fleeing: the prey walks or runs to escape
- dropping: the prey drops from the leaf
- wriggling: the prey wriggles to prevent capture
- attacking: the prey counter-attacks (or strikes back)
- no defence: the prey does not show any defensive mechanisms.

Fifteen replicates were carried out for each prey species and state (immobilized or not).

To evaluate *H. axyridis* feeding behaviour against the two prey species, searching and handling times were compared using a Wilcoxon test and attack rates using a likelihood ratio *G* test for immobilized and active prey separately. The proportions of each defensive mechanism used by the two prey were compared between prey species, for immobilized and active prey separately, using a likelihood ratio *G* test (SAS Institute, 2000).

Prey Suitability

In order to evaluate prey suitability, *H. axyridis* L3 developmental time (number of days before moulting to L4), weight gain (weight L4 – weight L3, as measured 0–12 h after each moult) and survival were evaluated. *Harmonia axyridis* individuals were taken 0–12 h after moulting to L3 and the experiment ended at the next moult. Prey species used were *H. vitripennis* (N3–N5) and *T. urticae* adults, both active and immobilized, provided *ad libitum*. Developmental time and weight gain were only recorded for individuals that successfully moulted to L4. Fifteen replicates were carried out for each prey species and state.

Two-way ANOVAs (prey species and mobility) were performed on developmental time and weight gain (Table I) and a G^2 test (likelihood ratio effect test) (prey species and mobility) was used to compare survival (SAS Institute, 2000).

Table I. Analysis of Variance and Likelihood Ratio Effect Test of the Effects of Prey Species (Intra- vs Extraguild Prey) and Mobility on Developmental Time, Weight Gain and Mortality of *Harmonia Axyridis*

Source of variation	<i>F</i>	df	<i>P</i>
Developmental time			
Model	9.04	3, 31	0.0002
Prey species	2.72	1	0.1102
Mobility	1.67	1	0.2047
Prey species * mobility	21.79	1	<0.0001
Weight gain			
Model	1.74	3, 31	0.1813
Prey species	1.78	1	0.1924
Mobility	0.16	1	0.6964
Prey species * mobility	1.95	1	0.1733
	<i>G</i>	df	<i>P</i>
Mortality			
Model	22.56	3	<0.0001
Prey species	10.32	1	0.0013
Mobility	7.70	1	0.0055
Prey species * mobility	13.33	1	0.0003

RESULTS

Prey Selection

Prey selection by *H. axyridis* was greatly affected by prey activity (Fig. 1). In the presence of active prey, all three *H. axyridis* attacks in the sequences were directed exclusively against *T. urticae* ($\chi_1^2 = 12.01$, $P < 0.0001$). However, in the presence of immobilized prey, attack frequency on *H. vitripennis* was 40%, 47% and 70% for the first, second and third prey consumed respectively (the mean attack frequency being 50%). In the first and second attacks prey selection corresponded to the relative prey abundance. The third attack and the total mean attack frequency showed a significant preference for *H. vitripennis* (attack 3: $\chi_1^2 = 5.51$, $P = 0.0169$; total attacks: $\chi_1^2 = 4.91$, $P = 0.0266$).

Components of Predation

Prey species had no influence on *H. axyridis* searching time when prey were immobilized (Wilcoxon test, $Z = 0.1245$, $P = 0.9009$). However, searching time was significantly longer in the presence of active *H. vitripennis* than in the presence of active *T. urticae* (Wilcoxon test,

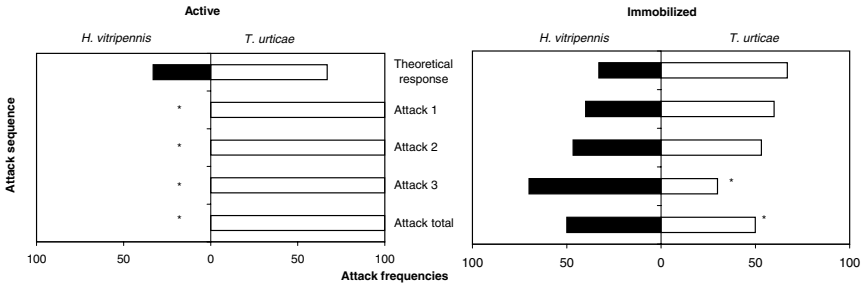


Fig. 1. Prey selection. Attack frequencies of *Harmonia axyridis* on immobilized and active *Hyaliodes vitripennis* and *Tetranychus urticae*. White areas represent predation on *T. urticae*, black areas represent show predation on *H. vitripennis*. Asterisks indicate a prey selection significantly different from the theoretical response (χ^2 , $P < 0.05$).

$Z = -3.6094$, $P = 0.0003$) (Fig. 2A). *Harmonia axyridis* capture rate was affected by prey activity: in the presence of immobilized prey, each attack was successful, while in the presence of active prey, capture rate was 13.3% for *H. vitripennis* and 100% for *T. urticae* (Fig. 2B) ($G_1 = 29.27$, $P < 0.0001$). The two prey species showed different defensive mechanisms: *T. urticae* did not use effective defensive mechanisms, while *H. vitripennis* escaped coccinellid attacks by fleeing in 87% of cases (Fig. 2B). *Harmonia axyridis* took significantly more time to consume *H. vitripennis* than to consume *T. urticae* (Fig. 2C) (Wilcoxon test: immobile prey, $Z = -4.6544$, $P < 0.0001$; active prey, $Z = 2.1830$, $P = 0.0290$).

Prey Suitability

Harmonia axyridis third instar development was affected by prey species and prey activity (Fig. 3A) (Table I). Developmental time was significantly longer when fed active *H. vitripennis* than when fed active *T. urticae* (ANOVA 1: $F_{1,12} = 13.27$, $P = 0.0039$). However, developmental time was longer when fed with immobilized *T. urticae* than with immobilized *H. vitripennis* (ANOVA 1: $F_{1,18} = 6.64$, $P = 0.0196$). Weight gain was not affected by prey species nor by prey activity (Fig. 3B) (Table I).

Harmonia axyridis larval mortality varied significantly according to prey species and prey activity (Fig. 3C) (Table I). Mortality rate was similar whichever prey species was offered as food when prey was active. However, the coccinellid mortality rate was significantly lower when fed with active *H. vitripennis* than with active *T. urticae* ($G_1 = 19.09$, $P < 0.0001$).

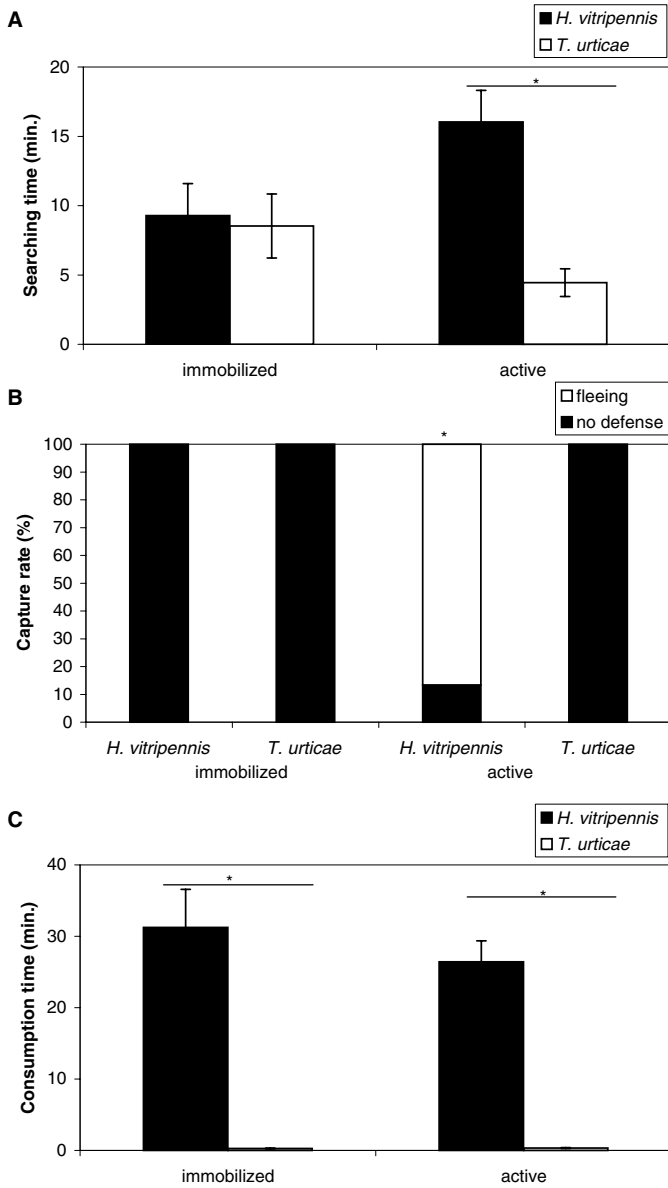


Fig. 2. Observations of components of predation. (A) Searching time; (B) Capture rate and defensive mechanisms of prey; and (C) Handling time of *Harmonia axyridis* when feeding on *Hyaliodes vitripennis* and *Tetranychus urticae*. Asterisks indicate a significant difference between the two prey species (ANOVA, $P < 0.05$).

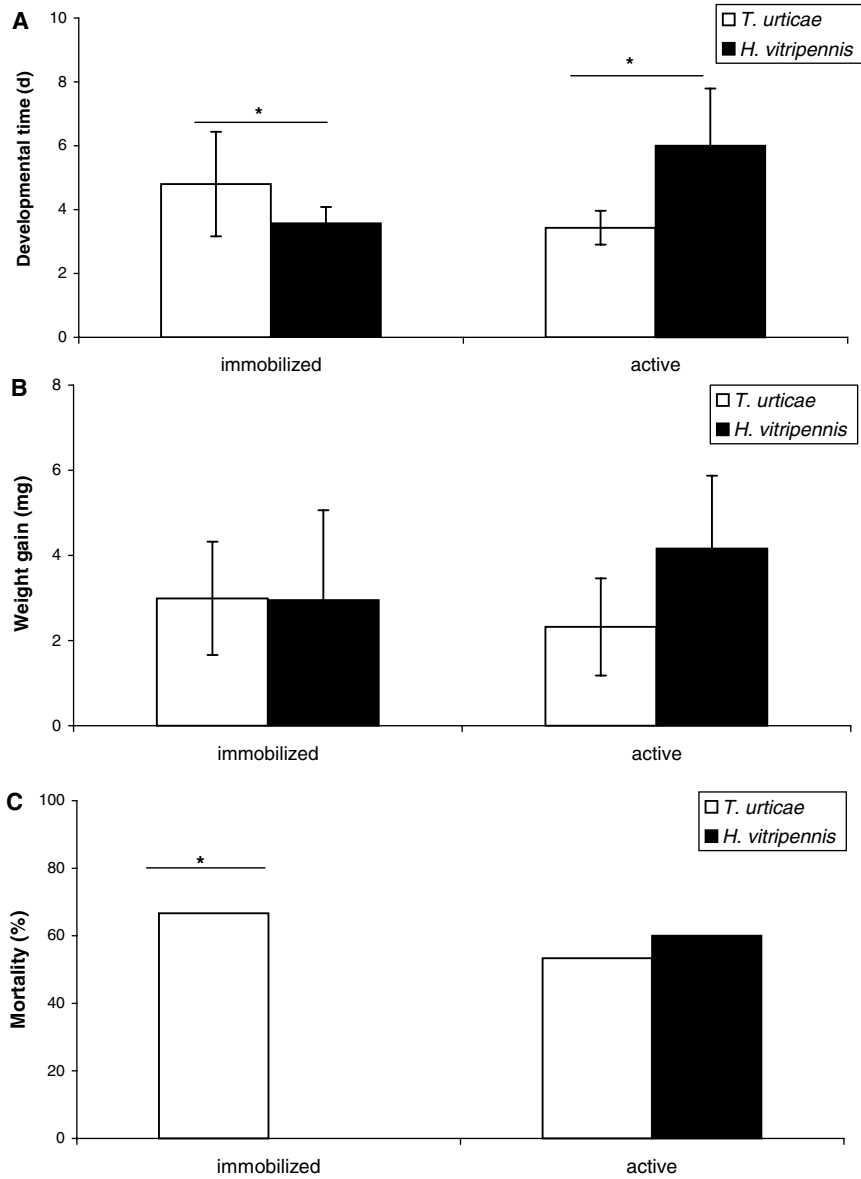


Fig. 3. Prey quality. (A) Developmental time; (B) Weight gain; and (C) Mortality of *Harmonia axyridis* feeding on immobilized and active *Hyaliodes vitripennis* and *Tetranychus urticae*. Asterisks indicate a significant difference between the prey species (ANOVA, $P < 0.05$; G test, $P < 0.05$).

DISCUSSION

The selection of prey by *H. axyridis* is greatly affected by prey activity. According to our predictions, the coccinellid attacked only the most vulnerable prey, *T. urticae*, in the presence of active prey, while it selected preferentially *H. vitripennis* in the presence of immobilized individuals.

Prey selection has previously been studied for coccinellids. Soares *et al.* (2004) observed that the prey preference of adult *H. axyridis aulica* differed between genders; no feeding preference was observed for the females in the presence of both *Myzus persicae* (Shulzer) and *Aphis fabae* Scopoli, while males showed a preference for *M. persicae*. The authors suggested that *H. axyridis* females present self-selection behaviour according to the basic criteria of Waldbauer and Friedman (1991), i.e. (i) the animal choice of food or nutrients is non-random, and (ii) the coccinellid benefits from self-selecting. As for males, prey preference may be correlated to prey size. Lucas *et al.* (1997) reported a preference of *H. axyridis* for *Aphis citricola* van der Goot when offered along with *T. urticae*. Veeravel and Baskaran (1995) evaluated prey preference for several life stages of *Coccinella transversalis* F. and *Cheilomenes sexmaculatus* F. and observed that only larval stages showed preference for a prey species. Thus, prey selection by Coccinellidae seems to vary according to the predator species, the predator stages and the prey species offered.

In the presence of active prey, *H. axyridis* was not able to capture *H. vitripennis* because the mirid was highly mobile and used effective defensive mechanisms to escape the attacks. Moreover, the high mobility of the mirid increased *H. axyridis* searching time and result in a longer developmental time and higher mortality rate. Prey mobility has already been considered as an important factor affecting prey selection (Sih and Christensen, 2001). Several studies have demonstrated that mobile prey generally increase foraging costs, reduce probability of capture and result in a lower net energetic gain for the predator (e.g. Allan *et al.*, 1987; Nordlund and Morrison, 1990). Prey defensive mechanisms could also influence prey selection. Roger *et al.* (2000) observed a reduced capture rate by *Coleomegilla maculata* (DeGeer) of prey with effective defensive responses. However, Soares *et al.* (2004) observed that *M. persicae* and *A. fabae* distribution and defensive strategies do not provide an advantage to any prey species facing *H. axyridis aulica* because the coccinellid searched and fed anywhere in the set-up.

Generally, prey size was correlated with nutrient gain, a large prey provide higher energetic gain than a small prey. For example, Houck (1991) demonstrated that the coccinellid *Stethorus punctum* (LeConte) selected its prey according to prey quality and nutritional needs. *Hyaliodes vitripennis*

is a larger prey than *T. urticae* and the prey quality experiment demonstrated that when considering only nutrient content, *H. vitripennis* provides a faster development for *H. axyridis* L3 and a lower mortality rate. Thus, *H. vitripennis* may be a food of high value for *H. axyridis* larvae and must be considered as a potential prey for the coccinellid.

Prey selection by an intraguild predator and prey value for this predator was evaluated by some authors. Depending on the species involved, different results have been observed: similar larval performance when fed with the extraguild and intraguild prey (Yasuda and Ohnuma, 1999; Lucas and Alomar, 2001) or the intraguild prey is an inferior or unsuitable food source for the intraguild predator (Phoofolo and Obrycki, 1998; Yasuda and Ohnuma, 1999). Thus, prey quality of intraguild and extraguild prey varies as a function of predator and prey characteristics and seems to be specific to each system.

Harmonia axyridis is an important generalist predator in apple orchard (Chouinard *et al.*, 1992, 2000). Under laboratory conditions, intraguild predation between this coccinellid and *H. vitripennis* is observed but does not reduce predation efficiency on phytophagous mites (Provost *et al.*, 2005). The intraguild prey, *H. vitripennis*, provides high quality nutrients to *H. axyridis*, but the high mobility and effective escape mechanisms reduce the relative prey quality. It is thus predicted that in apple orchards intraguild predation between these two mite predators should be rare and concentrated mainly during the mirid moulting periods, when fleeing is impossible.

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