

Prey preference of *Hyaliodes vitripennis* as an intraguild predator: Active predator choice or passive selection?

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Abstract

Prey vulnerability is a major factor influencing predator preferences. This study evaluated the preference of the glassy-winged mirid bug *Hyaliodes vitripennis* for two prey types: a slow-moving extraguild prey, the two-spotted spider mite *Tetranychus urticae*, and a faster intraguild prey, the phytoseiid mite *Amblyseius fallacis*. Tests were done in the presence of mobile and frozen individuals. Searching and handling time, defensive mechanisms and prey value of the two prey species were also evaluated. Results demonstrated that *H. vitripennis* had a constant preference for *T. urticae* over *A. fallacis* independently of prey mobility. Hence, *H. vitripennis* preference for *T. urticae* may be considered as an active predator choice rather than a passive selection. *H. vitripennis* searching time was longer in the presence of mobile prey than in the presence of the frozen prey regardless of the species. However, prey handling time was not affected by prey mobility. *T. urticae* did not show any effective defensive mechanisms to avoid the predator attacks while *A. fallacis* escaped 33.3% of the attacks by fleeing. Defensive mechanisms could reduce attack efficiency of *H. vitripennis* and increase its foraging costs. Evaluation of prey value showed that *T. urticae* provided higher weight gain and longer developmental time to *H. vitripennis*. *H. vitripennis* preference for *T. urticae* could be the result of nutritional suitability of this intraguild prey.

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1. Introduction

Generalist predators encounter several preys with different nutritional value and defensive mechanisms and the predator must develop several attack strategies to exploit a variety of preys. Optimal foraging theory predicts that the diet choice of a predator must maximize net nutrient gain and minimize energetic costs and predation risks (Stephen and Krebs, 1986). Facing two preys, the theory predicts that a predator will select the more profitable one to maximize its net energetic gain (Charnov, 1976; Stephen and Krebs, 1986). However, in some instance, the predator

does not act in accordance with the optimal foraging theory and readily attacks both preys.

A predator is classified as truly generalist when its prey selection is proportional to the relative abundance of the prey species in its environment (Begon et al., 1996). However, some predators show some preference, i.e., they preferentially select a prey over others, whatever the relative abundance of that prey (Cock, 1978; Hassell and Southwood, 1978). Food preference was observed for several insect predators (Cock, 1978) and has been identified as a species specific characteristic (Hassell and Southwood, 1978). Preference can affect regulation and interrelationships of populations, and even cause unstable predator-prey dynamic (Fryxell and Lunberg, 1994; Venzon et al., 2001). Prey selection by a predator may be attributed to one of two distinct mechanisms: active predator choice or passive selection (Pastorok, 1981; Stephen and Krebs,

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1986). Active choice occurs when a predator actively chooses a prey according to its nutritional value, while the prey physical and/or behavioral characteristics (mobility, size) do not influence the selection. On the other hand, passive selection is the result of predation opportunity based on prey physical and/or behavioral characteristics (vulnerability), rather than an active selection. For example, the mobility of different prey species may influence their encounter rates with a predator and thus influence their susceptibility to predation.

In Quebec apple orchards, phytophagous mites are important pests causing serious losses. Each season, two to three acaricide treatments are applied to manage these pests (Vincent and Bostanian, 1988). The use of a biological control agent may be an alternative to acaricide applications. The glassy-winged mirid bug, *Hyaliodes vitripennis* (Say) (Hemiptera: Miridae), and the phytoseiid mite *Amblyseius fallacis* (Garman) (Acarina: Phytoseiidae) are two important acarophagous predators in Quebec apple orchards that effectively control phytophagous mites (Brodeur et al., 1999; Chouinard et al., 1999, 2000). *H. vitripennis* is an active predator that mainly feeds on phytophagous mites and aphids (Brimah et al., 1982; Horsburgh, 1969; Kelton, 1983), but can also attack other arthropods such as predacious mites, leafhoppers and Lepidoptera (Horsburgh, 1969). An earlier study showed that the consumption of two-spotted spider mite, *Tetranychus urticae* Koch (Acarina: Tetranychidae), by *H. vitripennis* and *A. fallacis* resulted in a synergistic repressive effect on the shared prey when λ -cyhalothrin (pyrethroid) was applied (Provost et al., 2005). This study also showed the occurrence of intraguild predation by *H. vitripennis* feeding on *A. fallacis*.

Tetranychus urticae (the extraguild prey) and *A. fallacis* (the intraguild prey) have similar size (*T. urticae* adult: 0.3–0.4 mm, and *A. fallacis* adult: 0.33 mm), are both distributed on the entire apple tree, and have similar physiology (Chouinard et al., 2000). Nevertheless, *A. fallacis* is a major predator of *T. urticae* (Chouinard et al., 2000). Moreover, *H. vitripennis* and *A. fallacis* are present at the same period on the apple tree. That means that the intraguild predator is thus in the presence of this two possible preys and there is the potential for frequent interactions between *H. vitripennis* and *A. fallacis*.

Tetranychus urticae and *A. fallacis* have different mobility and defensive mechanisms: *A. fallacis* is a very active mite that walks to find prey mainly along the leaf veins, while *T. urticae* is less mobile, builds web and walks slowly (personal observations). Moreover, *A. fallacis* spends more time walking and moves faster than *T. urticae* (C. Provost, unpublished data). Sih and Christensen (2001) reviewed 134 studies and concluded that only prey mobility significantly explained variation in the concordance of observed diet patterns to optimal foraging theory. However, other studies have shown that prey defensive mechanisms may affect the prey selection by a predator as well. Effective defensive mechanisms could increase foraging costs and reduce energetic gain and attack success (Crawley, 1992).

Since *A. fallacis* has a higher mobility than *T. urticae*, the relative energetic gain resulting from predation on that prey may be lower. The present study evaluated the impact of prey vulnerability on *H. vitripennis* prey preference, and determined whether prey selection by the predator results from an active choice or passive selection. Moreover, the suitability of *T. urticae* and *A. fallacis* for *H. vitripennis* was determined. As *T. urticae* is less mobile than *A. fallacis*, we predict: (1), that *H. vitripennis* should prefer *T. urticae* in the presence of mobile prey; and (2), that *H. vitripennis* should select the two prey species in proportion of their relative abundances when these are immobilized.

2. Materials and methods

2.1. Biological material and experimental conditions

Hyaliodes vitripennis was collected in June in a commercial apple orchard in Rougemont (73°03' W, 45°26' N) Québec, Canada, and maintained in the laboratory 1–2 days on *Sitotroga cerealella* (Thomas) eggs, to avoid prior conditioning. Both prey species, *T. urticae* and *A. fallacis*, are naturally present in this orchard (C. Provost, unpublished data). The phytoseiid mite *A. fallacis* was obtained from a permanent rearing culture at Agriculture and Agri-Food Canada, St-Jean-sur-Richelieu, Québec. *A. fallacis* was reared on *T. urticae*. *T. urticae* was reared on Lima bean leaves, *Phaseolus lunatus* L. Rearing conditions for all arthropods were 20° ± 1 °C, 60–70% RH and a photoperiod of 16L: 8D. Preference experiments were performed on apple leaves, whose petioles were maintained in water for the experimental period. The experiments on *H. vitripennis* larval development were carried out on vertical apple shoots, with three terminal leaves. Each shoot was placed in a 4 L plastic box. Shoots and leaves were collected from trees in the same orchard and washed before the beginning of the experiment to eliminate other arthropods. Experimental conditions were 20° ± 1 °C, 60–70% RH and a photoperiod 16L: 8D. Before each test, individuals of *H. vitripennis* 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.

2.2. Preference experiments

Prey preference was determined for the 4th nymphal stage (N4) of the mirid *H. vitripennis*. This specific developmental stage was selected based on previous experiments showing that (1) levels of intraguild predation were similar between the different life stages tested (N2, N4, and adult) (Provost et al., 2005); (2) N4 was less affected by insecticide application than younger nymphal stages (Provost et al., 2003a,b); and (3) N4 is an interesting life stage from the point of view of biological control, as it is the most voracious stage and can be easily manipulated and introduced in apple orchard (Arnoldi et al., 1992; Brodeur et al., 1999; Chouinard et al., 1999). To evaluate the impact of prey mobility on

H. vitripennis prey preference, experiments were done in the presence of mobile and frozen prey. Frozen prey was freeze for 12 h before tests. Preliminary experiments demonstrated that frozen prey are as suitable as unfrozen ones, the mirid readily accepted the two prey types (frozen and unfrozen), and nymphal development was not affected by prey types (C. Provost, unpublished data). Each trial involved ten *A. fallacis* adults and ten *T. urticae* adults, placed randomly on an apple leaf. One *H. vitripennis* was introduced subsequently. Fourteen replicates were carried out for each treatment. Prey preference was determined by observations of the first three attacks. After an attack, the individual preyed upon was replaced by another individual in order to keep prey density and relative abundance constant. Attack frequency was determined as the percentage of *H. vitripennis* attack on a specific prey for each attack sequence. To determine prey preference, the attack frequency for each prey type was compared with a conformity test using the theoretical index of 50% representing no prey preference (SAS Institute, 2000). The impact of prey mobility on attack frequency was tested with a likelihood ratio *G* test for each prey species.

2.3. Searching and handling time

To evaluate *H. vitripennis* searching and handling time on *A. fallacis* and *T. urticae*, two additional parameters were recorded during the preference experiments: (1) searching time, i.e., the time delay between two attacks; and (2) handling time, the time from capture to the termination of feeding (determined as the moment when *H. vitripennis* removed its rostrum from the prey). The searching time and handling time were recorded for all attacks, regardless of the previous prey consumed. Observations were done on mobile and frozen preys. The effect of prey species and prey mobility on searching and handling time was evaluated using two-way ANOVA.

2.4. Defensive mechanisms of preys

Intraguild predator and prey developmental stages used for the observation of defensive mechanisms were the same as in the previous experiments. Fifteen adults of *A. fallacis* or *T. urticae* were placed on an apple leaf, and *H. vitripennis*

(N4) was subsequently introduced. Observation of defensive mechanisms was done following an attack. Defensive mechanisms were classified as either:

- Fleeing: the prey walks or runs away.
- Dropping: the prey drops from the leaf.
- No defense: no defensive mechanisms observable.

Moreover, the capture rate, i.e., in the proportion of an attack resulting in prey capture, was observed. Fifteen replicates were carried out. Proportions of each defensive mechanism were compared using a likelihood ratio *G* test and the percentages of mortality were compared between the two prey types using χ^2 test (SAS Institute, 2000).

2.5. Prey value

To evaluate the impact of prey mobility on prey value, *H. vitripennis* (N4) was fed with mobile and frozen prey. Individuals of *H. vitripennis* were taken 0–12 h after molting to N4 and the experiment ended by the next molting. Fresh prey was provided *ad libitum* to the predator each day. Three parameters were used to determine prey value:

- Developmental time: number of days before molting in N5.
- Weight gain: weight N5–weight N4, as measured in 0–12 h after each molt.
- Mortality (%): number of dead individuals.

Developmental time and weight gain were compared with two-way ANOVAs (prey type and mobility). Mortality of *H. vitripennis* on the two preys was compared using the G^2 test (likelihood ratio effect test) (prey type and mobility) (SAS Institute, 2000).

3. Results

3.1. Preference experiments

The attack frequency of *H. vitripennis* was significantly higher on mobile and frozen *T. urticae* than on *A. fallacis* ($\chi^2_{1,30}$, $P < 0.05$) (Fig. 1). *H. vitripennis* attack frequency on *T. urticae* was 80% for both mobile and frozen prey.

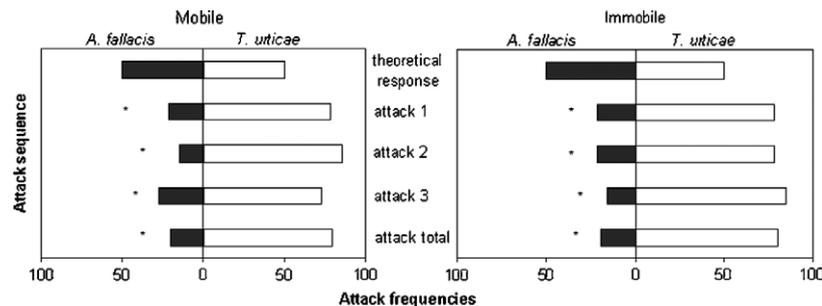


Fig. 1. Preference experiments. Attack frequencies of the mirid *Hyaliodes vitripennis* on mobile and frozen individuals of the phytoseiid mite *Amblyseius fallacis* (intraguild prey) and the two-spotted spider mite *Tetranychus urticae* (extraguild prey). White area show predation on the two-spotted spider mite, black areas show predation on the phytoseiid mite. Asterisks indicate a significant prey preference (χ^2 , $P < 0.05$).

This indicates that mobility does not affect prey preference ($G_1 = 0.013$, $P = 0.9110$).

3.2. Searching and handling time

Hyaliodes vitripennis searching time for *A. fallacis* was not different than for *T. urticae* (ANOVA2, model: $F_{3,79} = 2.6709$, $P = 0.0534$; prey type: $F_1 = 0$, $P = 0.9975$). However, we observed a higher searching time for mobile than frozen preys (ANOVA2, mobility: $F_1 = 6.7025$, $P = 0.0115$) (Fig. 2A). *H. vitripennis* handling time on *T. urticae* was approximately 1.5 times longer than on *A. fallacis* (ANOVA2, model: $F_{3,79} = 1.2130$, $P = 0.3108$; prey type: $F_1 = 3.4286$, $P = 0.0680$) and was not affected by prey mobility (ANOVA2, mobility: $F_1 = 0.1936$, $P = 0.6612$) (Fig. 2B).

3.3. Defensive mechanisms of preys

Hyaliodes vitripennis predation caused significantly higher mortality in *T. urticae* (100%) than in *A. fallacis*

(66.7%) ($\chi^2_{1,30} = 6.163$, $P < 0.0130$). *T. urticae* did not show any effective defensive mechanisms against *H. vitripennis* attacks. *A. fallacis* used fleeing as an effective defensive mechanism in 33.3% of the recorded interactions. The occurrence of defensive mechanisms was significantly greater in *A. fallacis* than in *T. urticae* ($G_1 = 7.938$, $P < 0.0048$).

3.4. Prey value

Hyaliodes vitripennis developmental time was significantly longer when fed with *T. urticae* than with *A. fallacis* (ANOVA2, prey type: $F_1 = 2.9043$, $P = 0.0208$), regardless of prey mobility (ANOVA2, mobility: $F_1 = 0.0033$, $P = 0.9363$) (Fig. 3A). Weight gain was superior when fed with *T. urticae* than with *A. fallacis* (ANOVA2, prey type: $F_1 = 5.94$, $P = 0.0187$) (Fig. 3B). Prey mobility did not influence *H. vitripennis* weight gain (ANOVA2, mobility: $F_1 = 0.1293$, $P = 0.7208$). *H. vitripennis* mortality was similar in all treatments (G^2 , $P > 0.05$).

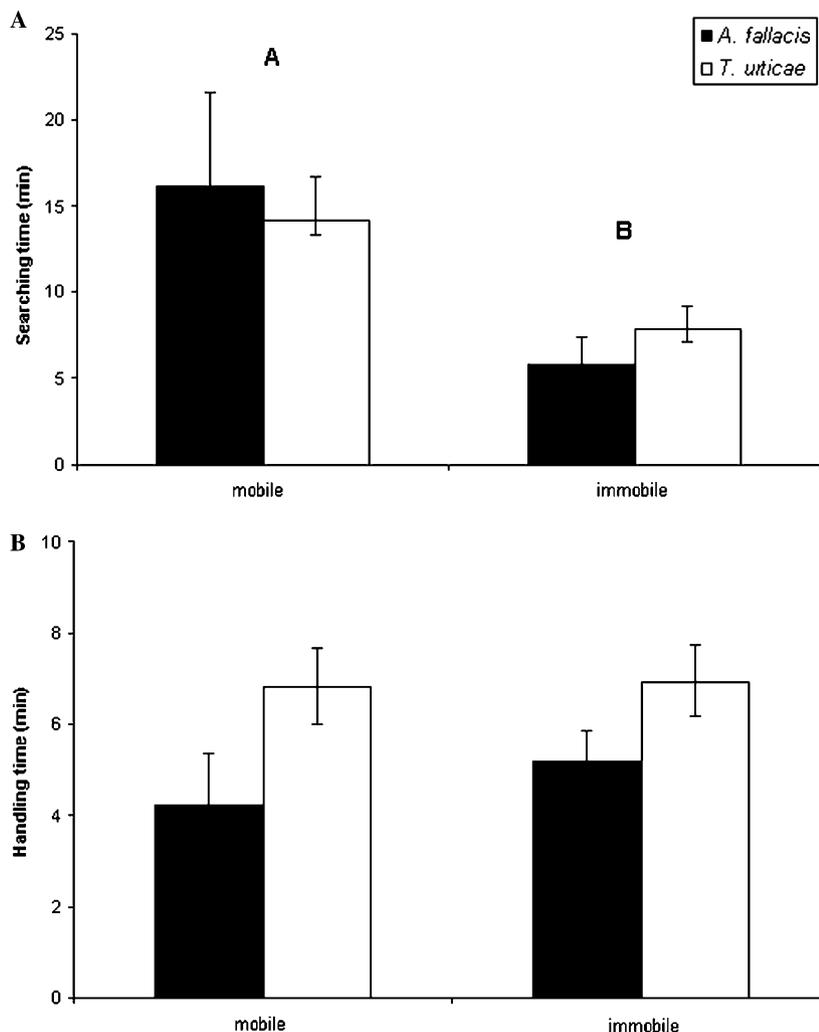


Fig. 2. Searching time (A) and handling time (B) of the mirid *Hyaliodes vitripennis* when feeding on mobile and frozen individuals of the phytoseiid mite *Amblyseius fallacis* (intraguild prey) and the two-spotted spider mite *Tetranychus urticae* (extraguild prey). Capital letters indicate a significant difference between prey species.

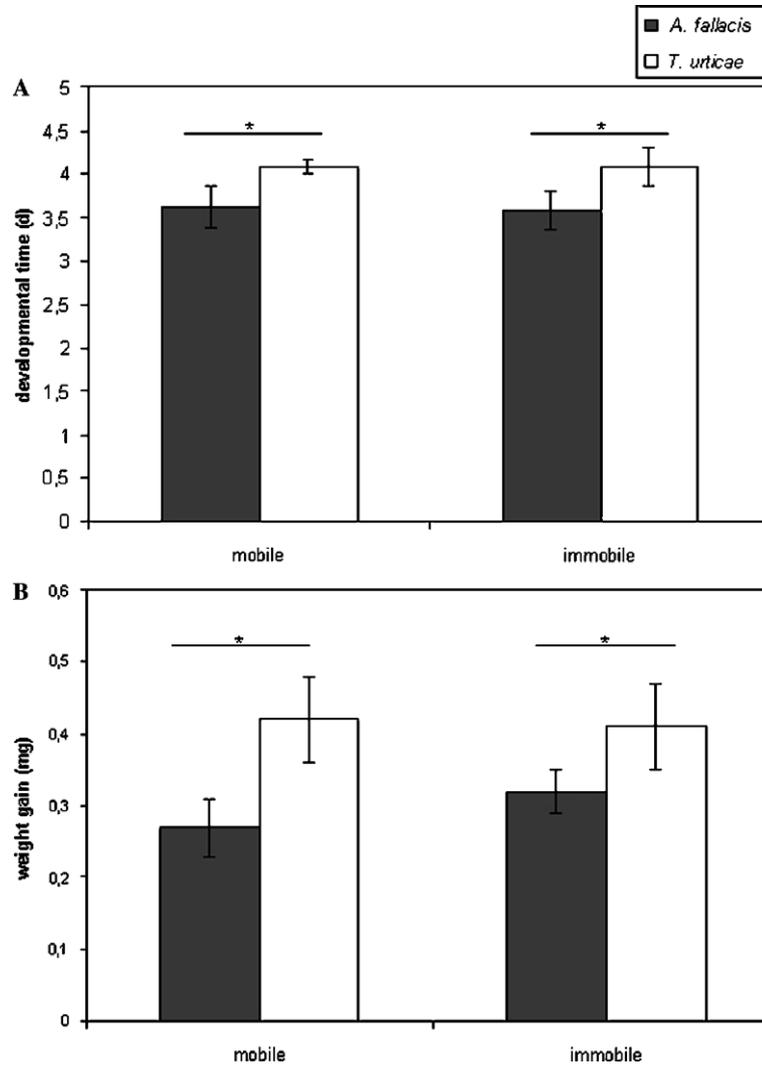


Fig. 3. Prey value. (A) Developmental time; and (B) Weight gain of the mirid *Hyaliodes vitripennis* feeding on mobile and frozen individuals of the phytoseiid mite *Amblyseius fallacis* (intraguild prey) and the two-spotted spider mite *Tetranychus urticae* (extraguild prey). *Indicate a significant difference between prey species.

4. Discussion

In the experiments with mobile prey, *H. vitripennis* preferred *T. urticae*, which is slower than *A. fallacis*. However, in the presence of frozen prey, *H. vitripennis* still selected *T. urticae* over *A. fallacis*. These results contrast with our prediction that *H. vitripennis* should select the two prey species in proportion of their relative abundances when immobilized. Therefore, *H. vitripennis* preference for *T. urticae* as a prey appears to be the result of an active predator choice rather than passive selection.

Previous observations of prey preference by predators were often related to the mobility and defensive mechanisms of the preys. High prey mobility and defensive mechanisms generally reduce encounter rate, increase handling time, reduce attack success and result in lower prey profitability (Crawley, 1992). In the presence of mobile prey, *H. vitripennis* preferentially selected *T. urticae*. This could be explained by the lower mobility and the absence of effective

defensive mechanisms of the extraguild prey. However, our results showed that prey mobility did not affect *H. vitripennis* prey selection. Several authors have observed that prey mobility (Allan et al., 1987; Eubanks and Denno, 2000; Molles and Pietruszka, 1987; Wratten, 1976) and defensive mechanisms of preys (Hagler and Cohen, 1991; Hajek and Dahlsten, 1987; Shimoda et al., 1997) affect prey selection and then result in a passive selection (Lang and Gsöld, 2001; Provost, in press). In an earlier study, we observed that *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) prey selection was influenced by defensive mechanisms of preys (Provost, in press). In the presence of mobile prey, the coccinellid selected *T. urticae* instead of *H. vitripennis*, even though this last species could procure a higher nutrient gain. However, in the presence of frozen prey, *H. vitripennis* was the selected prey.

In the presence of frozen prey, *H. vitripennis* showed a preference for *T. urticae*, which is contrary to our prediction. Two hypotheses are proposed to explain this unex-

pected result. First, prey selection probably affects the biology of the predator and consequently its fitness. *H. vitripennis* nymph 4 fed *T. urticae* yielded a higher body weight gain (which is generally considered as advantageous), but also a longer developmental time (which is considered to be disadvantageous). If the advantage of a high body weight outweighs that of a rapid development, then natural selection should have favor the selection of the prey that entitle high weight gain. Šešlija and Tucić (2003) observed that the development time of the bean weevil *Acanthoscelides obtectus* Say had an impact on its biology: longer developmental time resulted in higher body weight, higher fecundity and prolonged longevity. These characteristics would increase its fitness. However, slow growth will also have a negative effect on the intrinsic rate of population growth and the slow-growth high-mortality hypothesis predicts that longer developmental time would result in a higher mortality (Williams, 1999). Still, Williams (1999) also noted that on 10 studies involving Hemiptera, none supported the slow-growth high-mortality hypothesis.

Second, some authors suggested that the nutritional quality of a prey, or the specific nutrient needs of a predator, could explain predator preferences for some prey (Krebs and Davies, 1994; Tinbergen, 1981). For example, it is generally recognized that the nutrient contents of plants played a more significant role than energy in the evolution of herbivores diet selection (Owen Smith and Novellie, 1982; Rapport, 1980). Arthropod prey also contains specific nutrients that may influence the biology of a predator. Prey selection by some predators has been found to correlate with prey suitability in terms of impact on predator reproductive success or developmental time (Browne, 1995). Houck (1991) observed that females of the coccinellid *Stethorus punctum* (LeConte) selected mite eggs rich in lipids and proteins, over less nutritious mobile stages. Moreover, Evans et al. (2004) observed that the seven-spotted beetle, *Coccinella septempunctata* L., required aphids in their diets for egg production. It is possible that the preference of *H. vitripennis* for *T. urticae* is also based on nutrient content. Firlej (2002) had observed nymphal development of *H. vitripennis* on different diets and concluded that the addition of phytosterol to an artificial diet resulted in higher body weight, higher longevity and lower mortality when compared to the basic artificial diet. Phytosterol can be converted in cholesterol by phytophagous insects (Rees, 1985), while entomophagous insects generally cannot convert phytosterol.

Finally, we can also suppose that the higher weight gain of *H. vitripennis* when fed with *T. urticae* may be explained by a larger number of preys eaten by the predator. The difference in the number of prey consumed may be, at least in part, attributed to different handling times; *H. vitripennis* handling time was 1.5 times longer on *T. urticae* than on *A. fallacis*. Moreover, the presence of prey species in the field may also influence *H. vitripennis* prey selection and capture rate mainly by prior

exposure to *T. urticae*. *T. urticae* is an important prey, and preferred prey (Arnoldi et al., 1992), of the mirid and prey population density in apple orchard may be higher than *A. fallacis* (C. Provost, unpublished data).

The impact of intraguild predation on the success of biological control programs has often been debated. On the one hand, several authors believe that intraguild predators should have a positive impact of the natural suppression of pest, the intraguild predator may enhance pest suppression and intraguild predation may be favorable for the intraguild predator (e.g., Fagan and Denno, 2004; Matsumura et al., 2004). On the other hand, some authors have proposed that intraguild predation has a detrimental effect for biological control, because the intraguild predator disrupts the food web with negative consequences for pest suppression (e.g. Rosenheim and Corbett, 2003; Rosenheim et al., 2004). In this study, *H. vitripennis* selected the extraguild prey, *T. urticae*, instead of the intraguild prey, *A. fallacis*. Information on this prey preference is important for biological control. The use of *H. vitripennis* for biological control of *T. urticae* can be recommended, as this study indicates that the mirid predator will have no direct negative impact on the population of other predatory mites like *A. fallacis*.

In conclusion, *H. vitripennis* prey preference does not seem to be determined by prey vulnerability: prey preference was an active choice rather than a passive selection. Previous studies have shown that *H. vitripennis* is a voracious acarophagous predator (Arnoldi et al., 1992; Brodeur et al., 1999; Chouinard et al., 1999), compatible with pyrethroids (Provost et al., 2003a,b), and that low levels of intraguild predation were observed with other acarophagous predators in apple orchards (Provost, in press). Finally, this study has shown that *H. vitripennis* prefers to feed on *T. urticae* which is a positive point for its use in integrated pest management programs.

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