# Voracity and feeding preferences of two aphidophagous coccinellids on *Aphis citricola* and *Tetranychus urticae*

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## Abstract

Voracity and feeding preferences of adult *Coccinella septempunctata* L. and *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae, tribe Coccinellini) were evaluated in the laboratory on a common prey, the spirea aphid, *Aphis citricola* van der Goot (Homoptera: Aphididae), and on the twospotted spider mite, *Tetranychus urticae* Koch (Acarina: Tetranychidae), a prey previously unrecorded for these two predators. The experiments were carried out in the laboratory on apple saplings (*Malus domestica* Borkhausen). Adult males and females of *H. axyridis* consumed significantly more mites than adults of *C. septempunctata*. For *H. axyridis*, males consumed 41.3 spider mites in 24 h and females 48.4, whereas for *C. septempunctata* males consumed 14.1 prey and females 15.2. The consumption of spirea aphids by the males was similar for the two species. Consumption by the females was significantly greater for *H. axyridis* (46.5) than for *C. septempunctata* (22.2). The two coccinellids showed a significant preference for *A. citricola* in the presence of *T. urticae*. This preference was more pronounced for *C. septempunctata*. The total number of prey consumed and the percentage of exploited biomass decreased significantly for *C. septempunctata* and stayed relatively constant for *H. axyridis* as the number of mites increased in the prey ratio. Our results suggest that *T. urticae* is only an alternative prey for both predators, and that *H. axyridis* should be more efficient than *C. septempunctata* in a prey assemblage with aphids and mites.

### Introduction

Measuring the voracity of predators is an important step in assessing the potential of a biological control agent. However, for generalist predators, the simultaneous presence in nature of numerous pest species can invalidate results obtained in an experimental setting with a single prey species. Therefore, it is important to know the feeding preferences of the predator. Predaceous coccinellids generally accept a large number of prey species and frequently show a preference for one species (Hodek, 1973). Hodek (1973) and Majerus (1994) proposed a classification system of preys, i.e., (1) essential preys allowing egg maturation, oviposition and complete development, (2) accepted but inadequate preys (and alternative preys) that do not allow egg maturation or normal levels of oviposition but prolong survival, (3) rejected preys (not accepted), and (4) toxic preys that kill ladybirds. The prey choice, normally directed towards the optimal prey, could also be directed towards an alternative prey, or even a toxic prey (Hodek, 1973; Majerus, 1994).

Assessing coccinellid preference by presenting the two prey species in equal numbers is an incomplete test because the predator's response is strongly influenced by the ratio of the two preys presented (Murdoch, 1969). When tested with different prey ratios, a predator can show four types of response, viz., (1) a constant preference for one prey species, (2) no preference, when the ratio of consumed prey is equal to the ratio of prey individuals in the environment (i.e., null switching) (Chesson, 1984), (3) a switching behaviour, when the predator eats disproportionally more of the more abundant prey (Murdoch, 1969), (4) an anti-switching behaviour, when the predator eats disproportionally more of the less abundant prey (Chesson, 1984).

The seven-spotted lady beetle, Coccinella septempunctata L., is widely spread in apple orchards from Hungary (Radwan & Lövei, 1982), Poland (Niemczyk & Pruska, 1986), Belgium (Hemptinne & Naisse, 1988), and Quebec (Canada) (Tourneur et al., 1992; Chouinard et al., 1992). C. septempunctata is of palearctic origin and it was released in the United States on several occasions between 1956 and 1971 (Gordon & Vandenberg, 1991). Since then, this eurytopic predator (Iperti, 1991) had a geographical expansion in the United States and southern Canada (Schaefer et al., 1987). Stenophagous and principally aphidophagous, C. septempunctata consume the five aphid species found in apple orchards (Angalet et al., 1979; Bouchard et al., 1982; Iablokoff-Khnzorian, 1982; Olszack, 1988).

*Harmonia axyridis* Pallas originates from the Far East. This coccinellid was recently introduced into North America and is now established in southern Louisiana and eastern Mississippi (Chapin & Brou, 1991), and in Quebec, Canada (Coderre et al., 1995). This large-sized arboreal lady beetle (Iablokoff-Khnzorian, 1982), that has a fecundity superior to the majority of other coccinellids (Hukusima & Kamei, 1970 in Hodek, 1973), is often found in apple orchards (Hodek, 1973). More polyphagous than *C. septempunctata*, it feeds on numerous aphid species in different cultures (Hodek, 1973; Schanderl et al., 1985), on scale insects (McClure, 1987) and on psyllids (Iablokoff-Khnzorian, 1982).

The aim of this study was to compare the voracity, the feeding preference and the predation efficiency of a stenophagous and a polyphagous coccinellid on their usual preys, and on a prey previously unrecorded for the two predators. Prey acceptability by the predators and voracity towards the two preys were evaluated and compared.

## Materials and methods

*C. septempunctata* adults were collected in a wheat field in the Montreal  $(73^{\circ}36' \text{ W}, 45^{\circ}30' \text{ N})$  (Quebec, Canada) area, and *H. axyridis* adults (population of Chinese origin) are from a mass rearing on *Ephestia kuehniella* Zeller eggs (Lepidoptera: Pyralidae). The two coccinellids were then reared on *A. citric*-

*ola* at 25 °C, 70% r.h. and a L16:D8 photoperiod for one month. The twospotted spider mite, *Tetranychus urticae* Koch, was mass reared on Lima bean plants, *Phaseolus limensis*. The spirea aphid, *Aphis citricola* van der Goot, was collected from apple orchards located near Sainte-Hyacinthe (72°56' W: 45°39' N) and Deux-Montagnes (73°53' W: 45°31' N) (Quebec, Canada).

The experiments were carried out on four- to sixweek old apple saplings (McIntosh cultivar) grown in a greenhouse and cleared of all arthropods before the experiments. The saplings with five equally-sized and undamaged leaves were then fixed with Plasticine in a hole pierced in the bottom of a plastic container (8 cm high with a 15 cm diameter). This container was placed in a second plastic container with water to keep the roots wet.

Adult beetles (2–4 weeks old) were used. They were fed *ad libitum* and were then starved for 24 h before the experiment. Adult mites and immature aphids (third larval stage) were placed on the leaves of an apple sapling. After five minutes the predator was placed on the plant. The set up was hermetically sealed with a transparent, plastic film, and placed in an incubator (25  $^{\circ}$ C, 70% r.h., L16:D8) during 24 h.

After 24 h, the set ups were placed in a refrigerator for 15 min. The unconsumed preys were counted with a binocular microscope according to Sabelis (1985). Each experiment was replicated 30 times and included a control set up containing only preys. Analyses were carried out on the data adjusted with the control treatments using the following equation:

$$C = C_1 - T$$

with C = number of prey consumed after 24 h,  $C_1$  = number of prey not found in the test, and T = number of prey not found in the control set up.

*Voracity.* In the first experiment, predator voracity on the spider mites was measured. Each replicate consisted of two treatments: one *H. axyridis* with 60 spider mites and one *C. septempunctata* with 60 spider mites. In the second experiment, the two treatments consisted one adult *H. axyridis* with 100 aphids and one adult *C. septempunctata* with 100 aphids. In both experiments, the mean number of prey consumed was compared with a Mann–Whitney U test. The mean values for each species were compared with respect to males, females, and between two morphs of *H. axyridis*.

To evaluate the biomass consumption of each predator, 90 third-instar aphid larvae and 250 spider-mite adults were weighed. The average weight obtained for each prey was then multiplied by the number of prey consumed by each individual.

*Feeding preferences and predation efficiency.* Three treatments, corresponding to three different ratios of prey, were presented to *C. septempunctata* or *H. axyridis*, enclosed in an experimental set up as previously described. Each replicate contained the following treatments: one adult predator with 40 spider mites and 20 aphids, one adult predator with 30 spider mites and 30 aphids and one adult predator with 20 spider mites and 40 aphids.

For feeding preferences, the dependent variable was the consumed spider mite ratio, i.e., the number of spider mites consumed over the total number of prey consumed. The first series of statistical analyses was carried out separately for the two predators. For the three treatments (mites/aphids: 20/40, 30/30, 40/20), the consumed spider mite ratios were compared to the proposed spider mite ratios. Confidence intervals of the mean consumed spider mite ratios were calculated at  $\alpha = 0.05$ . The proposed spider mite ratio was then compared to the confidence interval of the corresponding consumed spider mite ratio (Sokal & Rohlf, 1981). The second series compared the feeding preferences of C. septempunctata and H. axyridis. The mean consumed spider mite ratios were compared with a three-way ANOVA (prey ratio, predator species and predator sex) using Manly's preference index (Sokal & Rohlf, 1981; Manly et al., 1972). Cock (1978) stated that Manly's preference index was the only method that took into account the prey densities depletion by predation during experiments. Reviewing the literature on food preference, Sherratt & Harvey (1993) concluded accordingly.

Manly's preference index:

 $a = (r_1/n_1)/(r_1/n_1 + r_2/n_2)^*$ 

with  $r_1$  = proportion of prey type 1 in the predator diet (here  $r_1 = T$ . *urticae*),  $n_1$  = proportion of prey type 1 available (0.33, 0.50, 0.67), and  $r_2$  = proportion of prey type 2 in the predator diet (here  $r_2 = A$ . *citricola*).

The predation efficiency was estimated from the total number of prey consumed for each initial ratio, and the percentage of prey biomass consumed by the predator. For each of these two parameters, two-way ANOVA was used, comparing (1) sex (male vs female) and (2) species and initial ratio density (1) C7-20/40, (2) C7-30/30, (3) C7-40/20, (4) C7-60/0, (5) Ha-20/40,

(6) Ha-30/30, (7) Ha-40/20, (8) Ha-60/0) (Sokal & Rohlf, 1981). The total biomass of prey consumed by each predator was compared with a one-way ANOVA (Sokal & Rohlf, 1981).

Proportions were arcsin  $\sqrt{x}$  transformed (Sokal & Rohlf, 1981). Only the untransformed values are presented. All statistical tests were carried out with the SuperANOVA software (Abacus Concepts Inc. 1991).

## Results

*Voracity.* In 24 h, *H. axyridis* females consumed significantly more spider mites than *C. septempunctata* females (Mann-Whitney, U = 0, df=18, 8, P=0.0001) (Table 1). *H. axyridis* males consumed significantly more spider mites than did *C. septempunctata* males (Mann-Whitney, U = 15, df=12, 22, P=0.001). There was no significant difference in the consumption by red and black morphs (Mann-Whitney, U = 65.5, df=8, 22, P=0.291).

*C. septempunctata* females consumed less aphids in 24 h than did *H. axyridis* females (Mann-Whitney, U = 32, df=21, 7, P=0.028) (Table 2). Consumption by males was not significantly different among species (Mann-Whitney, U=28.5, df=4, 18, P=0.53). The voracity of *H. axyridis* red morphs was similar to that of the black morphs (Mann-Whitney, U = 36.5, df=4, 21, P=0.68).

The mean (n = 30) A. *citricola* weight was 0.1497 mg, whereas that of *T. urticae* (n = 100) was 0.0167 mg. Third-instar aphid larvae were 8.96 times heavier than a tetranychid adult.

*Feeding preferences.* For all analyses, no significant differences between the sexes or morphs were found. The percentage of spider mites consumed by *C. septempunctata* was significantly less than the percentage of available spider mites (Figure 1A). The results were similar for *H. axyridis*. The percentage of spider mites consumed by *H. axyridis* was also significantly less than the percentage of available spider mites (Figure 1B). The mean Manly's index was significantly higher for *H. axyridis* (0,290) than for *C. septempunctata* (0,197) (ANOVA, F = 4.76, df=1, P=0.031) (Table 3).

*Predation efficiency.* For all analyses, no significant differences between sexes or morphs were found. The total number of prey consumed differed significantly according to predator species and prey ratio (ANOVA,

Table 1. Voracity of adult Harmonia axyridis and Coccinella septempunctataon Tetranychus urticae (n = 60), on apple saplings

Predator	T. urticae a	T. urticae adults consumed during 24 h			
	Number	Number		Biomass (mg)	
	Mean	s.d.	Mean	s.d.	
Male					
H. axyridis	41.3 (b)*	11.7	0.690 (b)	0.195	
C. septempunctata	14.1 (a)	11.7	0.235 (a)	0.195	
Female					
H. axyridis	48.4 (b)	4.7	0.808 (b)	0.078	
C. septempunctata	15.2 (a)	9.8	0.254 (a)	0.164	
H. axyridis – Morph					
red	38.6 (a)	13.8	0.645 (a)	0.230	
black	44.9 (a)	9.2	0.750 (a)	0.154	

s.d. = standard deviation.

\*For a given column and subsection, different letters indicate significant differences (Mann–Whitney,  $\alpha$ =0.05).

Table 2. Voracity of adult Harmonia axyridis and Coccinella septempunctata on Aphis citricola (n = 100), on apple saplings

Predator	A. citricola adults consumed during 24 h			
	Number		Biomass (mg)	
	Mean	s.d.	Mean	s.d.
Male				
H. axyridis	26.2 (a)*	20.1	3.92 (a)	3.01
C. septempunctata	18.8 (a)	16.6	2.81 (a)	2.49
Female				
H. axyridis	46.5 (b)	26.4	6.96 (b)	3.95
C. septempunctata	22.2 (a)	13.4	3.32 (a)	2.01
H. axyridis – Morph				
red	39.6 (a)	33.1	5.93 (a)	4.96
black	30.4 (a)	22.4	4.56 (a)	3.35

s.d. = standard deviation.

\*For a given column and subsection, different letters indicate significant differences (Mann–Whitney,  $\alpha$ =0.05).

*Table 3.* Manly's preference index for different ratios of *Tetranychus urticae* over total prey proposed (*Tetranychus urticae* and *Aphis citricola*) for *Coccinella septempunctata* and *Harmonia axyridis* 

Proposed	Manly's pre	Manly's preference index			
T. urticae	H. axyridis	H. axyridis		C. septempunctata	
	Mean	s.d.	Mean	s.d.	
0.33 (20/60)	0.317	0.157	0.208	0.187	
0.50 (30/60)	0.265	0.152	0.206	0.236	
0.67 (40/60)	0.308	0.152	0.192	0.135	
All ratios pooled	0.297 (a)*	0.154	0.202 (b)	0.189	

s.d. = standard deviation.

\*Different letters indicate significant differences between means (ANOVA,  $\alpha = 0.05$ ).

Proposed	Number of prey consumed		% of total biomass exploited*	
T. urticae	Mean	s.d.	Mean	s.d.
ratio (numbers)**				
H. axyridis				
0.33 (20/60)	45.35 (a)***	11.01	71.2 (a)	19.7
0.50 (30/60)	43.93 (ab)	10.29	73.8 (a)	15.8
0.67 (40/60)	38.92 (bc)	12.79	75.6 (a)	13.9
1.00 (60/60)	43.20 (ab)	10.73	71.1 (a)	17.9
C. septempunctata				
0.33 (20/60)	36.11 (c)	14.77	59.2 (b)	27.9
0.50 (30/60)	29.04 (d)	12.81	51.0 (b)	29.8
0.67 (40/60)	25.68 (d)	8.61	58.0 (b)	19.5
1.00 (60/60)	14.73 (e)	10.43	23.6 (c)	17.4

Table 4. Total number of prey and percentage of total biomass consumed in 24 h by Coccinella septempunctata and Harmonia axyridis on apple saplings, for different ratios of Tetranychus urticae

s.d. = standard deviation.

\*Ratio of consumed biomass over offered biomass.

\*\*number of *T. urticae* over total number of prey proposed i.e., *T. urticae* and *Aphis citricola*. \*\*\*Different letters indicate significant differences between means in the same column

(ANOVA,  $\alpha$ =0.05).

F = 23.33, df=7, P=0.0001). For *H. axyridis*, values ranged from 45.3 preys for a ratio of 20 mites/40 aphids to 38.9 for the ratio 40 mites/20 aphids, and the only significant difference found was between these extreme values (LSD, P=0.045). For C. septempunctata, the total number of prey consumed decreased gradually as the proportion of mites increased. The total number of prey consumed given a ratio of 20 mites/40 aphids was significantly larger than all other ratios. The total number of prey consumed for the ratio of 60 mites/no aphid was significantly less than the total number consumed for the others ratios (Table 4). The total biomass eaten by the two predators decreased significantly when the ratio of proposed spider mites increased (ANOVA, F = 52.22, df=7, P=0.0001) (Table 5).

The percentage of exploited biomass was significantly different between treatments (ANOVA, F = 18.60, df=7, P=0.0001). For *C. septempunctata*, the percentage obtained with the treatment 60 mites/no aphid was significantly lower than for the other treatments. However, consumption by *H. axyridis* did not differ when the ratio of proposed spider mite biomass increased.

### Discussion

Prey acceptance and prey suitability are two important factors in prey selection. Prey acceptance is determined by the capture success of the predator and by its acceptance or rejection of the prey after 'tasting'. Our study reports for the first time acceptance of *T. urticae* by *H. axyridis* and *C. septempunctata*. Predation on *T. urticae* occurred even in the presence of aphids. For *H. axyridis*, mites represented (in terms of consumed preys) 23 to 45% of its diet depending on the ratio offered, and 14 to 30% for *C. septempunctata*, indicating that the prey is accepted.

Prey acceptance does not necessarily imply that the prey is suitable (Hagen, 1987), and Coccinellids can accept inadequate preys, even toxic ones (Blackman, 1967; Hodek, 1973; Majerus, 1994; Iablokoff-Khnzorian, 1982; Formusoh & Wilde, 1993; Hodek & Honêk, 1988). Putman (1957) tested the suitability of *T. urticae* as a food resource for ten coccinellid species. Only *Coleomegilla maculata lengi* Timberlake (a very polyphagous species) developed normally on this prey. The other species, including two species of the genus *Coccinella (C. transversoguttata* Fald. and *C. trifasciata perplexa* Mulsant) either refused the prey or ate only a small number of preys after being deprived of food. This and the fact that the total number of preys and the percentage of biomass exploited



*Figure 1.* Ratio of *Tetranychus urticae* consumed in 24 h on apple saplings, with 95% confidence intervals. (A) by *Coccinella septempunctata*, (B) by *Harmonia axyridis*. Ratio = n/(n + m); where n = number of *T. urticae* individuals and m = number of *Aphis citricola* individuals. The theoretical ratio corresponds to no feeding preference. No overlapping of the theoretical ratio and confidence interval lines indicates a significant preference.

decreased with the increase of mites available in the system suggest that *T. urticae* could be an unsuitable prey for *C. septempunctata*. *C. septempunctata* and *Adalia bipunctata* L. larvae fed with unsuitable prey consumed less preys and had a lower feeding rate than larvae fed with suitable prey (Blackman, 1967). However, although Putman (1957) found that larvae could not develop normally solely on a diet of spider mites, coccinellids in an agrosystem could probably develop on a mixed diet constituting partly of two spotted spider mites.

Table 5. Total biomass consumed in 24 h by *Coccinella* septempunctata and *Harmonia axyridis* on apple saplings, for different ratios of *Tetranychus urticae* (*T. urticae* over total prey proposed; *T. urticae* and *Aphis citricola*)

Proposed	Total biomass consumed (mg)		
T. urticae	Mean	s.d.	
ratio (numbers)*			
H. axyridis			
0.33 (20/60)	4.503 (e)**	1.248	
0.50 (30/60)	3.683 (d)	0.789	
0.67 (40/60)	2.770 (c)	0.511	
1.00 (60/60)	0.712 (a)	0.179	
C. septempunctata			
0.33 (20/60)	3.745 (d)	1.765	
0.50 (30/60)	2.544 (bc)	1.490	
0.67 (40/60)	2.123 (b)	0.714	
1.00 (60/60)	0.237 (a)	0.174	

s.d. = standard deviation.

\*Number of *T. urticae* over total number of prey proposed, i.e., *T. urticae* and *Aphis citricola*.

\*\*Different letters indicate significant differences between means (ANOVA,  $\alpha = 0.05$ ).

The feeding preferences of the predators reflect their mainly aphidophagous diet and suggest that the spider mite constitutes only an alternative prey, particularly for *C. septempunctata*. *H. axyridis* is considered more polyphagous (Ongagna et al., 1993) than *C. septempunctata* (Iablokoff-Khnzorian, 1982).

The observed preference could result (1) from differential searching rates, (2) from different times spent in various habitat types, (3) from rejection of one of the prey types after encounter, or (4) from differing abilities of prey to escape (Hassel, 1978). Putman (1957) found that nine out of ten coccinellid species tested consumed less attractive prey (mites in this study), but did not switch from extensive to intensive search behaviour. This could have occurred with the two coccinellid species in our experimental set up. In our experiments, rejection of spider mites was not observed. While foraging for preys, ladybirds tend to follow prominent leaf veins (Dixon, 1959) and aphids generally form colonies close to these veins. Spider mites were more dispersed on leaves, and thus the probability of encounter with a foraging coccinellid was probably lower. Furthermore, most generalist predators select their preys according to their relative size (Sabelis, 1992). Due to their relative (compared to the coccinellid predator) small size spider mites could have been overlooked by ladybirds. Escaping abilities

of prey should be also important. The lower mobility of aphids, and the fact that one of their main escaping behaviours, the dropping technique, was not efficient in the small cages, could lead to a greater capture success.

Among insects, several studies have shown that a previous feeding experience could modify subsequent feeding behaviour. Food selection and preference could be influenced by a previous exposure to one food type in phytophagous species (de Boer & Hanson, 1984; Eijsackers & van Lanteren, 1970; Hanson, 1983; Papaj & Prokopy, 1989), and in parasitoids (Jansson & Lashomb, 1988; Mandevile & Mullens, 1990; Thorpe & Jones, 1937; van Alphen & Vet, 1986). Conditioning for prey preference by predator species, occurs rarely. It was shown for an Odonata larva (Blois & Cloarec, 1985) and for an acarophagous ladybird (Houck, 1986). Before our experiments, coccinellids were reared on aphids. This could have influenced their prey selection in favour of aphids.

Switching did not take place in our experiment. Similarly, working with coccinellids and two aphid species, Murdoch & Marks (1973) did not find switching behaviour. Coccinellids were found to use a different hunting behaviour against mobile or sedentary aphids (A. Ferran, pers. comm). Given the size, displacement and behavioural differences between spider mites and aphids, one should expect that searching behaviour may differ for the two preys. Obata (1986) has shown that H. axyridis detects its prey with visual and olfactory cues. According to Murdoch & Marks (1973), switching will most likely occur when predators show a searching behaviour when the two preys are different, or when the predators have to hunt differently to get each species. It is possible that switching behaviour could append at much higher ratios of prey, particularly with the polyphagous predator H. axyridis. Lawton et al. (1974), working with the aquatic predator Notonecta glauca L. (Hemiptera: Notonectidae), have shown that the switching behaviour appeared progressively along the ten days of the experiment, the predator requiring a learning period in order to increase the proportion of successful attacks against the more numerous preys. The duration of our experiment could have been too short in this respect.

The elytral pattern of Coccinellidae depends on many factors. In *H. axyridis*, the number and size of elytral spots depends on the temperature prevailing at the pupal stage, while coloration is genetically determined. The genes responsible for beetle coloration also affect the physiology and the ecology of the insect (Komaî, 1964 in Iablokoff-Khnzorian, 1982). In our experiments, the black morph was dominated by the *spectabilis* Fald., *conspicua* Fald. and *tripunctata* Tan. phenotypes, and the red morph by *succinea* Hope (Komaï, 1964 in Iablokoff-Khnzorian, 1982). Voracity, feeding preferences and predation efficiency in a two-prey system were similar for the different morphs.

This study showed the high voracity of *H. axyridis* against aphids and mites, and suggested the possible use of this coccinellid in biological control programs against these pests in apple orchards by inundative releases. In apple orchards, the two predators may consume spider mites even in the presence of aphids. However, the biomass eaten by the two coccinellids decreased when more spider mites were available, thereby revealing that the coccinellids could not compensate the lost biomass by eating more prey. The impact of predators is technically difficult to assess *in situ*. Laboratory tests should then be completed by studies in the field and special concern should be given to the impact of the release of this exotic species on indigenous coccinellids.

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