

# Suitability of *Aphis fabae*, *Myzus persicae* (Homoptera: Aphididae) and *Aleyrodes proletella* (Homoptera: Aleyrodidae) as prey for *Coccinella undecimpunctata* (Coleoptera: Coccinellidae)

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## Abstract

The suitability of *Aphis fabae* Scopoli, *Myzus persicae* Sulzer and *Aleyrodes proletella* L. as food sources for *Coccinella undecimpunctata* L. was evaluated by studying the impact of prey consumption on the predator's population growth parameters and feeding parameters. Unlike *A. proletella*, *A. fabae* and *M. persicae* supported the development and reproduction of *C. undecimpunctata*. *A. fabae* and *M. persicae* were considered to be essential prey, whereas *A. proletella* was considered to be an alternative prey. Aphid species showed different degrees of suitability: *M. persicae* significantly decreased the pre-oviposition period and increased adult longevity, fecundity and fertility compared with *A. fabae*. Moreover, *A. fabae* represents a suitable diet for larval development, but is not a suitable food source for adult reproduction. The predator's population growth parameters,  $R_0$ ,  $r_m$  and  $\lambda$  were increased with *M. persicae*, whereas  $T$  decreased. We found that the 4th instar larvae were the most voracious, particularly when fed on *M. persicae*; nevertheless, with this prey daily weight gain and feeding efficiency of 4th instar larvae were similar to that of individuals fed with *A. fabae*.

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**Keywords:** *Coccinella undecimpunctata*; *Aphis fabae*; *Myzus persicae*; *Aleyrodes proletella*; Prey suitability; Feeding efficiency; Population growth parameters

## 1. Introduction

Predator diet specificity, feeding preferences and capacity for population increase are all factors that largely depend on prey suitability (Dixon, 2000). Quantitative data on the main developmental parameters (such as development times, survival and reproductive capacity) indicate whether the prey is essential (ensures the completion of larval development and oviposition) or alternative (serves just as a source of energy and thus prolongs survival) (Evans et al., 1999; Hodek and Honěk, 1996; Kalushkov and Hodek, 2001). Essential foods show varying degrees of favourability, enabling different development rates, survival and fecundity. Alternative foods may range from highly toxic to quite suitable, enabling survival in periods of

scarcity of essential food (Evans et al., 1999; Hodek and Honěk, 1996). In spite of their considerable polyphagy, coccinellids are highly specific as far as essential food is concerned (Soares et al., 2004, 2005). Therefore, studying the range of essential prey for coccinellids is an important step in understanding their potential as biological control agents against a given pest (Dixon, 2000; Hodek and Honěk, 1996; Obrycki and Orr, 1990; Tsaganou et al., 2004).

*Coccinella undecimpunctata* L. (Coleoptera: Coccinellidae) is a euriphagous predator, which prefers to feed on aphids (Hodek and Honěk, 1996; Raimundo and Alves, 1986). This lady beetle is established in the Azores and has potential to be a biological control agent against aphids (ElHag, 1992; Zaki et al., 1999).

*Aleyrodes proletella* L. (Homoptera: Aleyrodidae), *Aphis fabae* Scopoli and *Myzus persicae* Sulzer (Homoptera: Aphididae) are three important pests of Azorean

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agricultural systems, causing significant damage to horticultural plants, either in the field or in greenhouses. *Aphis fabae* is a polyphagous cosmopolitan pest (Blackman and Eastop, 2000; Dixon, 1998; Ilharco, 1982). It is one of the best-known pests of agrarian ecosystems, causing damage to wheat fields and horticultural plants (Minks and Harrewijn, 1989). The green peach aphid, *M. persicae*, is found worldwide threatening many economically important plants (horticultural to ornamental), mainly due to the transmission of plant viruses (Blackman and Eastop, 2000; Minks and Harrewijn, 1989). Unlike *A. fabae*, *M. persicae* is considered to be a suitable prey species for many coccinellids, such as *Adalia bipunctata* L. and *Coccinella septempunctata* L. (Coleoptera: Coccinellidae) (Blackman, 1967). The cabbage whitefly, *A. proletella*, is a polyphagous species that is found in temperate regions; it causes direct and indirect damage to horticultural plants, especially in greenhouses (Martin, 1999). As these three pests may be simultaneously present in assorted horticultural crops (such as of cabbage, sweet potato, lettuce, pumpkin), either in fields or greenhouses, we evaluated the suitability of *A. fabae*, *M. persicae* and *A. proletella* as food sources for *C. undecimpunctata* in this study. Prey suitability was evaluated by studying the impact of prey consumption on the predator's population growth parameters (survival and development time of larvae, and longevity and reproductive performance of adults) and feeding parameters (voracity, daily biomass consumption, daily weight gain and feeding efficiency).

## 2. Materials and methods

### 2.1. Insects

Adults of *C. undecimpunctata* were collected in Sta. Maria Island, Azores, Portugal, during early July 2004, before experiments took place. Lady beetles were reared at  $22 \pm 1$  °C,  $75 \pm 5\%$  relative humidity (RH) and at a photoperiod of 16 h light/8 h dark, using fluorescent lamps (Philips ref. TDL 23W/54 and TDL 18W/54). Insects were fed an *ad libitum* supply of aphids that were at different developmental stages (*A. fabae* and *M. persicae*), pollen and honey. The mixed diet was provided to avoid food adaptation (Rana et al., 2002) and to supply a wider group of nutrients to the predator. Colonies of *A. fabae* and *M. persicae* were reared on *Vicia faba major* L. at  $15 \pm 1$  °C and  $75 \pm 5\%$  RH. *Aleyrodes proletella* was reared on *Brassica oleracea* L. at  $25 \pm 1$  °C and  $75 \pm 5\%$  RH. The photoperiod was 16 h light/8 h dark, using fluorescent lamps (Philips ref. TDL 23W/54 and TDL 18W/54).

### 2.2. Prey suitability: population growth parameters

The influence of *A. fabae*, *M. persicae* and *A. proletella* on the population growth parameters of *C. undecimpunctata* was evaluated by measuring survival rate and development

time of immatures, and longevity and reproductive performance of adults. The net reproductive rate [ $R_0 = \sum l_x m_x$ ], intrinsic rate of natural increase [ $r_m = \ln R_0(T)^{-1}$ ], finite rate of increase [ $\lambda = e^r$ ] and mean generation time ( $T$ , the sum of development time from the egg stage to half of the life expectation of females after sexual maturation) were estimated (Krebs, 1994; Southwood and Henderson, 2000). Experiments regarding population growth parameters started during August 2004. All assays were performed at  $25 \pm 1$  °C,  $75 \pm 5\%$  RH, with a photoperiod of 16 h light/8 h dark, under fluorescent lamps (Philips ref.: TDL 23W/54 e TDL 18W/54).

#### 2.2.1. Development time and survival rate of immature stages

Pre-imaginal development time and survival were estimated by observing the individuals twice a day, from egg (laid by adults fed with single diets) to emergence of the adult. Lady beetles were isolated in cylindrical plastic boxes (diameter: 3 cm, height: 1 cm) and fed *ad libitum* with single diets of either *A. fabae*, *M. persicae* and *A. proletella*. The number of replicates was 35, 30 and 75 for *M. persicae*, *A. fabae* and *A. proletella*, respectively.

#### 2.2.2. Longevity and reproductive performance

To evaluate longevity and reproductive performance of the adults, individuals were sexed and paired. Each pair was placed inside a 60-ml cylindrical plastic box (diameter: 5 cm, height: 3 cm) and fed *ad libitum* single diets of either *A. fabae*, *M. persicae* or *A. proletella*. Each couple was observed daily to record the longevity, and egg clusters were removed twice a day. Pre-oviposition period, oviposition period, fecundity (number of laid eggs), fertility (number of hatched eggs) and percentage of eggs hatching (fertility/fecundity) were determined. The number of replicates was of 35, 30 and 75 for *M. persicae*, *A. fabae* and *A. proletella*, respectively.

### 2.3. Prey suitability: feeding parameters

The suitability of *A. fabae*, *M. persicae* and *A. proletella* as food sources for *C. undecimpunctata* was evaluated by measuring voracity, daily biomass consumption, daily weight gain and feeding efficiency, for all the developmental stages of the predator using single diets. Individuals were isolated in 60-ml plastic boxes and supplied twice a day (09:00 and 17:00) with apterous females of *A. fabae* or *M. persicae*, or 3rd instar larvae of *A. proletella*. The number of prey supplied depended on the developmental stage of the predators: 30 individuals (09:00: 10, 17:00: 20), 50 (20, 30), 70 (30, 40), 90 (40, 50) and 90 (40, 50) for 1st, 2nd, 3rd, 4th instars and adults (during their sexual maturation period), respectively. Experimentation started simultaneously with the assays from Section 2.2. (August 2004). All assays were performed at  $25 \pm 1$  °C,  $75 \pm 5\%$  RH, with a photoperiod of 16 h light/8 h dark, under fluorescent lamps (Philips ref.: TDL 23W/54 e TDL 18W/54). For each test, the number of replicates was  $>10$ .

### 2.3.1. Voracity and daily biomass consumption

For each treatment, the number of prey alive was recorded twice a day (09:00 and 17:00) after the predation periods given above. The weight of prey and predators was recorded twice a day (09:00 and 17:00) (using a  $10^{-4}$  mg Mettler AM50 analytic balance), before and after prey consumption. Natural mortality of the aphids and whiteflies was monitored in the absence of predators (control treatments), in a similar experimental set-up and with identical abiotic conditions.

Voracity ( $V_o$ ) was determined according to the following model (Soares et al., 2004):

$$V_o = (A - a_{24})ra_{24}$$

where,  $V_o$  = number of prey eaten,  $A$  = number of prey available,  $a_{24}$  = number of prey alive after 24 h and  $ra_{24}$  = ratio of prey found alive after 24 h in the control treatment (number of aphids remaining alive/total number of aphids kept in the plastic boxes for 24 h).

According to Soares et al. (2004), body weights of *A. fabae* and *M. persicae* are different (the mean body weight of an *A. fabae* wingless female is 1.09 mg, whereas that of a *M. persicae* wingless female is 0.48 mg), thus coccinellid satiation could be reached after consumption of a different number of prey items. Therefore, daily biomass consumption (DBC) was evaluated using the methodology of Shanderl (1987), based on the following model:

$$DBC_{(mg)} = (W_i/N)V_oPUC$$

where,  $DBC_{(mg)}$  = daily biomass consumption,  $W_i$  = total weight of prey provided,  $N$  = number of prey provided,  $V_o$  = number of prey eaten and PUC = prey utilisation coefficient.

The prey utilization coefficient (PUC) is the proportion of prey consumed and it was only estimated for aphids. For *A. prolella*, PUC was considered to be equal to 1, as only fully-consumed nymphs were regarded as being fed. To estimate the *C. undecimpunctata* PUC of aphid prey, the following control tests were carried out: 15 individuals of each stage were placed individually in contact with only one aphid (*A. fabae* or *M. persicae*) for 6 h, inside 7-ml cylindrical plastic boxes (diameter: 3 cm, height: 1 cm). To calculate consumption rates, each aphid was weighed before and after being in contact with the predator. Partially consumed or sucked aphids were considered as being fed.

### 2.3.2. Daily weight gain and feeding efficiency

Weight increase following predation is a good indicator of energy intake and associated costs (Frazer, 1988). We evaluated the 24-h weight gain (DWG) of larvae and adults within the sexual maturation period, after being fed on *A. fabae*, *M. persicae* or *A. prolella*. Adult body weight was evaluated individually using a Mettler AM 50 analytical balance with a precision of  $10^{-4}$  mg.

Feeding efficiency (FE) was evaluated as follows (Soares et al., 2005):

$$FE = (DWG/DBC_{(mg)})100$$

### 2.4. Statistical analysis

Samples were first described as regular averages and standard errors. Analyses of variance (ANOVA) were conducted on all data, except for survival rates. Where statistical differences existed between data sets ( $P < 0.05$ ), Fisher's least significant difference (LSD) tests were used to separate the differing means (Zar, 1996). Survival rates were analysed using multiple comparison test for proportions, where significant results are represented by giving a  $q_{0.05,\infty,3}$  value  $> 3.314$ . To reduce variance differences, data concerning the percentage of egg hatching were transformed by arcsine  $\sqrt{(x)}$ , and development time, pre-oviposition period, oviposition period, fecundity, fertility, voracity and biomass consumption were transformed by  $\sqrt{(x+0.5)}$  (Zar, 1996). All the analyses were performed using SPSS 12.0.1 Windows (SPSS Inc, 2003).

## 3. Results

### 3.1. Prey suitability: population growth parameters

#### 3.1.1. Development and survival of immature stages

With the exception of pre-pupae and pupae, the development times of *C. undecimpunctata* immature stages that were fed with *A. prolella* were significantly longer than those fed with *A. fabae* or *M. persicae* (Fig. 1). Hence, the total development time of the immature stages displayed statistically significant differences among aphid prey species and whiteflies (Fig. 1). Eggs from adults reared in the single prey treatments and 4th instars, had development times that were significantly longer when the predator was fed *A. fabae* than *M. persicae* (Fig. 1).

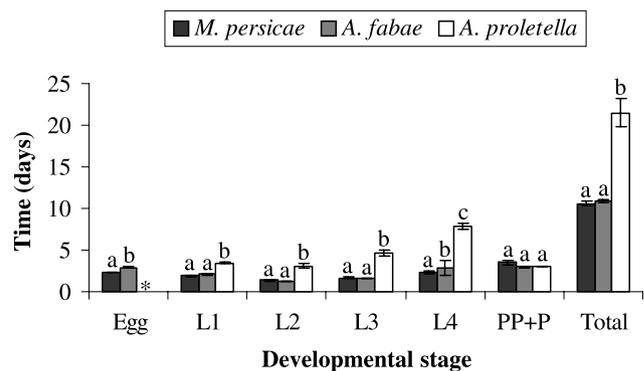


Fig. 1. Pre-imaginal development time (days  $\pm$  SE) of *Coccinella undecimpunctata* fed on single diets of *Aphis fabae*, *Myzus persicae* or *Aleyrodes prolella*. Legend: L<sub>1</sub>, L<sub>2</sub>, L<sub>3</sub>, and L<sub>4</sub>—first, second, third and fourth larval instars, respectively; PP+P, prepupa and pupa. Means in each column for each developmental stage followed by different letters are significantly different at  $P < 0.05$  (LSD tests). \*Not estimated since females fed with *A. prolella* did not oviposit.

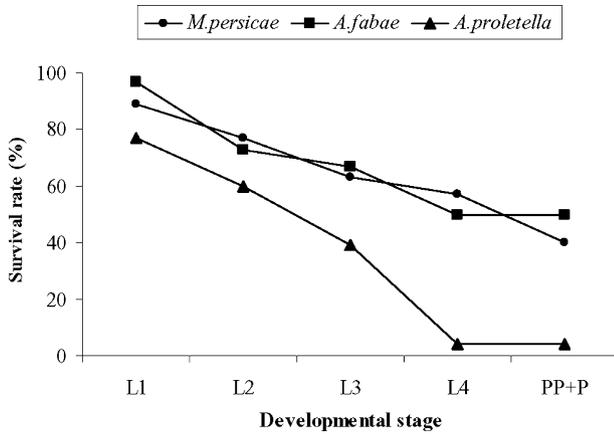


Fig. 2. Survival rates of *Coccinella undecimpunctata* pre-imaginal stages fed on single diets of *Aphis fabae*, *Myzus persicae* or *Aleyrodes proletella*. Legend: L<sub>1</sub>, L<sub>2</sub>, L<sub>3</sub>, and L<sub>4</sub>—first, second, third and fourth larval instars, respectively; PP+P, prepupa and pupa.

Accumulated survival rates when lady beetles were fed *M. persicae* (40%) or *A. fabae* (50%) were significantly higher than when fed *A. proletella* (4%) ( $q = 6.56$  and  $q = 7.51$ ,  $P < 0.05$ , respectively, for *M. persicae*/*A. proletella* and *A. fabae*/*A. proletella* comparisons, Fig. 2).

3.1.2. Longevity and reproductive performance

Concerning adult longevity, there were significant differences between the diets: longevity was significantly higher when *M. persicae* was the prey and shorter when lady beetles were fed with *A. proletella* (Table 1).

The pre-oviposition period was significantly higher when *C. undecimpunctata* was fed *A. fabae* compared with *M. persicae*. However, oviposition period was similar among the aphid diets (Table 1). Regarding the reproductive performance, both *A. fabae* and *M. persicae* had high values of fecundity. Fecundity and fertility were significantly higher when *C. undecimpunctata* was fed *M. persi-*

*cae*, but there were no significant differences in the percentage of eggs hatching between these prey species. *Coccinella undecimpunctata* females that were fed *A. proletella* did not oviposit (Table 1).

*M. persicae* showed a higher potential to increase the population of *C. undecimpunctata*, causing a  $R_0$  that was over two times greater than that of *A. fabae*; it also showed higher  $r_m$  and  $\lambda$  values. On the other hand, *A. proletella* did not enable predator sustainability; this was particularly due to their lack of ability to reproduce when fed on this prey (Table 2).

3.2. Prey suitability: feeding parameters

3.2.1. Voracity and daily biomass consumption

All *C. undecimpunctata* stages consumed *M. persicae* and *A. fabae*; the 4th instar larvae were the most voracious. For this larval instar, the number of prey consumed was significantly higher when *M. persicae* was the prey; nevertheless, as *M. persicae* had, on average, lower biomass than *A. fabae*, biomass consumption was significantly lower when the green peach aphid was the prey (Fig. 3A and B).

Table 2

Population growth parameters of *Coccinella undecimpunctata* fed on single diets of *Aphis fabae*, *Myzus persicae* or *Aleyrodes proletella*.  $R_0$ , net reproductive rate;  $r_m$ , intrinsic rate of natural increase;  $\lambda$ , finite rate of increase;  $T$ , mean generation time

Parameters	Prey		
	<i>A. fabae</i>	<i>A. proletella</i>	<i>M. persicae</i>
$R_0$	143.28	0	342.34
$r_m$	0.16	0	0.20
$\lambda$	1.17	0	1.22
$T$	31.02	0	29.64

Table 1

Longevity, pre-oviposition and oviposition periods (days  $\pm$  SE), and reproductive parameters [fecundity (number of laid eggs  $\pm$  SE); fertility (number of hatched eggs  $\pm$  SE); percentage of hatching (percentage of hatched eggs  $\pm$  SE)] of *Coccinella undecimpunctata* fed on single diets of *Aphis fabae*, *Myzus persicae* or *Aleyrodes proletella*

Parameters	Prey			Anova
	<i>A. fabae</i>	<i>A. proletella</i>	<i>M. persicae</i>	
Longevity				
Female	30.36 $\pm$ 4.93a	14.88 $\pm$ 2.09b	30.10 $\pm$ 2.87a	$F_{(2,34)} = 9.51$ ; $P = 0.001$
Male	25.73 $\pm$ 2.84b	12.25 $\pm$ 0.94a	44.90 $\pm$ 7.35c	$F_{(2,34)} = 19.46$ ; $P \leq 0.0001$
Adults	28.05 $\pm$ 2.82b	13.56 $\pm$ 1.15a	37.50 $\pm$ 4.20c	$F_{(2,34)} = 26.58$ ; $P \leq 0.0001$
Pre-oviposition period	7.0 $\pm$ 1.04a	—	4.40 $\pm$ 0.27b	$F_{(1,19)} = 5.97$ ; $P = 0.025$
Oviposition period	20.9 $\pm$ 4.78a	—	24.6 $\pm$ 3.04a	$F_{(1,19)} = 1.02$ ; $P = 0.315$
Fecundity (Fec)				
Total	194 $\pm$ 49.86b	0.00 $\pm$ 0.00a	596.20 $\pm$ 118.52c	$F_{(2,33)} = 64.95$ ; $P \leq 0.0001$
Fertility (Fer)				
Total	151.00 $\pm$ 37.66a	—	353.20 $\pm$ 70.23b	$F_{(1,19)} = 11.83$ ; $P = 0.003$
$Fer_{(oviposition\ period/2)}$	58.14 $\pm$ 13.80a	—	213.65 $\pm$ 53.96b	$F_{(1,19)} = 1157$ ; $P = 0.003$
Percentage of egg hatching (%)				
Total	78.42 $\pm$ 2.6a	—	68.00 $\pm$ 10.48a	$F_{(1,19)} = 0.53$ ; $P = 0.48$

Different letters within a row indicate significant differences (Fisher’s Protected LSD test;  $P < 0.05$ )—Not estimated since females fed with *A. proletella* did not oviposit.

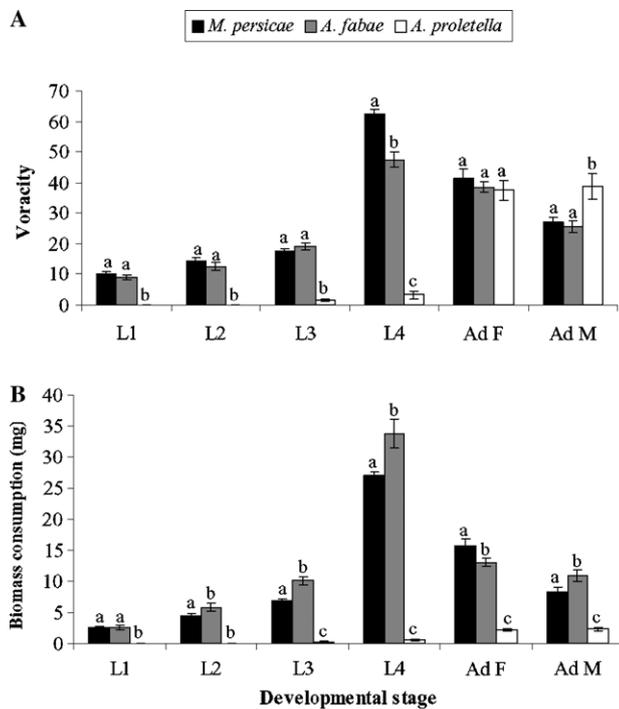


Fig. 3. (A) Daily voracity (number of prey eaten  $\pm$  SE) and (B) daily biomass consumption (mg of aphids eaten  $\pm$  SE) of *Coccinella undecimpunctata* larval instars (L<sub>1</sub>, L<sub>2</sub>, L<sub>3</sub> and L<sub>4</sub>) and adults (Ad F, females; Ad M, males) fed on single diets of *Aphis fabae*, *Myzus persicae* or *Aleyrodes proletella*. Means in each column for each developmental instars followed by different letters are significantly different at  $P < 0.05$  (LSD test).

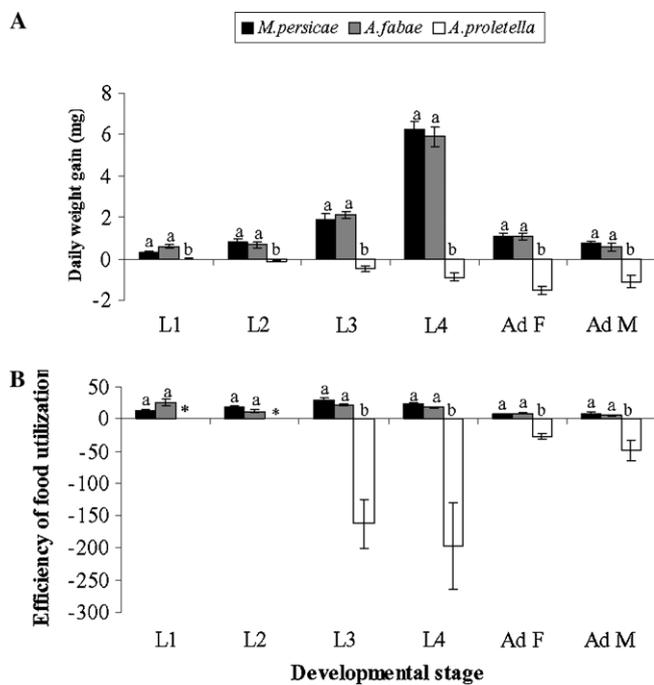


Fig. 4. (A) Daily weight gain (mg  $\pm$  SE) and (B) feeding efficiency (% of weight gain over biomass consumption per day  $\pm$  SE) of *Coccinella undecimpunctata* larval instars (L<sub>1</sub>, L<sub>2</sub>, L<sub>3</sub> and L<sub>4</sub>) and adults (Ad F, females; Ad M, males) fed on single diets of *Aphis fabae*, *Myzus persicae* or *Aleyrodes proletella*. Means in each column for each developmental instars followed by different letters are significantly different at  $P < 0.05$  (LSD test). \*Not estimated since individuals did not consume *A. proletella*.

Larvae of *C. undecimpunctata* consumed a very low number of *A. proletella*. This was in contrast to adults that ate almost the same quantity of whiteflies compared with aphid preys; however, biomass consumption was significantly lower (Fig. 3A and B).

### 3.2.2. Daily weight gain and feeding efficiency

All *C. undecimpunctata* stages increased their weight to a similar extent when fed *M. persicae* and *A. fabae* (Fig. 4A). Although the adults ate *A. proletella*, their weight was decreased, resulting in a negative feeding efficiency (Fig. 4A and B). Feeding efficiency did not differ significantly between the single diets of aphids (Fig. 4B).

## 4. Discussion

The study of development time, survival and reproductive performance of lady beetles, as well as the voracity and physiological basis of food utilization with different prey, allows the evaluation of the suitability of food sources. Several authors have shown that food quality affects the development time and survival of lady beetle larvae (Blackman, 1967; Işıkber and Copland, 2002; Kalushkov, 1998; Kalushkov and Hodek, 2001, 2004; Obrycki and Orr, 1990), as well as affects the parameters of reproductive performance of the adults, such as fecundity, fertility and percentage of hatching (Blackman, 1967; Hodek, 1993; Michaud, 2005; Nijima and Takahashi, 1980; Nijima et al., 1986). Our results showed that, although survival rates were relatively low, *A. fabae* and *M. persicae* are equally suitable prey for the pre-imaginal stages of *C. undecimpunctata*, as no considerable differences in the total development times and survival were observed. ElHag and Zaitoon (1996) have observed higher survival rates of *C. undecimpunctata* (61.5%). However, they used a mixed diet of two other aphids [*Brevicoryne brassicae* (L.) and *Rhopalosiphum padi* L. (Homoptera: Aphididae)]. *Aleyrodes proletella*, on the other hand, was shown to be less suitable, as the total development time of the predator almost doubled and survival was severely reduced. The single developmental stage that did not present significant differences was the pupa—a fact that also supports the idea that the pupal development time depends mainly on metabolic rates, whereas larval development is also dependent on prey quality (Honěk and Kocourek, 1990). Tsaganou et al. (2004) also found that the development time of *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) pupae were not affected by prey species. Regarding reproductive performance and adult longevity, we found that *A. proletella* did not allow the reproduction of *C. undecimpunctata* and significantly reduced the longevity, indicating that this species is a food source of low suitability. The higher fertility, fecundity and adult longevity, as well as the lower pre-oviposition period, with *M. persicae*, indicate that this prey is more suitable for *C. undecimpunctata* adults than *A. fabae*. Our results agree with Michaud's (2005) suggestion that

larvae and adults of coccinellids may differ in nutritional requirements. For instance, *A. fabae* and *M. persicae* displayed equal suitability to larval stages but differed in suitability to adults. Indeed, *M. persicae* presents higher  $R_0$  and  $r_m$  values than *A. fabae*, resulting in a higher number of offspring within an identical period, despite of the absence of differences between diets for the pre-imaginal development. Moreover, our  $R_0$  and  $r_m$  values were much higher than those obtained by ElHag and Zaitoon (1996) when feeding *C. undecimpunctata* with a mixed diet of *B. brassicae* and *R. padi*. These differences are a consequence of a longer mean development time (20.6 days) and lower fecundity ( $370.05 \pm 8.3$ ) that were observed by these authors, suggesting that this diet was less suitable for *C. undecimpunctata* than was the single diet of *M. persicae*. Nevertheless, the survival of the pre-imaginal stages was similar to that obtained in our study with *M. persicae*.

Predator voracity was similar between the aphid species, but biomass consumption of *A. fabae* was higher. This fact could be related to the higher biomass of *A. fabae*, which is twice the weight of *M. persicae*. However, there were no differences in daily weight gain and feeding efficiency, suggesting that, for the same body-weight increase, *C. undecimpunctata* needs to consume more biomass of *A. fabae* than of *M. persicae*. Soares et al. (2005) also observed that daily weight gain of *H. axyridis* was not affected by these two aphid species. Differential biomass consumption is perhaps indicative of aphid palatability and of the ability of lady beetles to show a marked preference (Omkar, 2005), which arises as a result of differences in chemical constitution (cuticular waxes or nutritive), morphology and/or defensive behaviour of aphids (Dixon, 2000; Hodek, 1993; Olszak, 1988). Differences in biomass quality may lead predators to increase their consumption of low-quality prey to obtain less abundant nutrients. Our results indicate that an equal pattern exists for aphid biomass consumption by males and larvae (i.e., higher with *A. fabae*), but that it is inverted in females (i.e., higher with *M. persicae*); this is probably due to the differential nutritive requirements for egg maturation. *Coccinella undecimpunctata* 4th larval instars were the most voracious, regardless of the aphid species. Although the adults ate *A. proletella*, their weight was not increased, resulting in a negative feeding efficiency; therefore, the low suitability of this prey for *C. undecimpunctata* was shown.

Comparison of the biological parameters and, consequently, the population growth parameters of *C. undecimpunctata*, suggests that, from an ecophysiological point of view, *M. persicae* and *A. fabae* are essential prey species and *A. proletella* is an alternative prey. Moreover, our results suggest that both aphid species differ in the degree of favourability. Nevertheless, generalist predators, such as lady beetle adults, consume alternative as well as essential prey, which probably enhances their ability to capitalize on short-lived and scattered opportunities as they seek out suitable sites in which to reproduce (Evans

et al., 1999). In terms of biological control, alternative prey are particularly important for sustaining coccinellid populations that survive largely on aphid species that exhibit 'boom and bust' cycles of abundance, as they can function to reduce local extinction events when essential prey are scarce (Michaud, 2005).

## References

- Blackman, R.L., 1967. The effects of different prey on *Adalia bipunctata* L. and *Coccinella 7-punctata* L. Ann. Appl. Biol. 59, 207–219.
- Blackman, R.L., Eastop, V.F., 2000. Aphids on the world's Crops: An identification and information guide, second ed. The Natural History Museum, London.
- Dixon, A.F.G., 1998. Aphid Ecology. Chapman and Hall, London.
- Dixon, A.F.G., 2000. Insect predator–prey dynamics: ladybirds and biological control. Cambridge University Press, Cambridge, MA.
- ElHag, E.T.A., 1992. Potential Role of indigenous Coccinellidae in regulation of aphid populations in Central Arabia wheat fields. Trop. Pes. Mgmt 38 (4), 425–430.
- ElHag, E.T.A., Zaitoon, A.A., 1996. Biological parameters for four coccinellid species in Central Saudi Arabia. Biol. Control 7, 316–319.
- Evans, E.W., Stevenson, A.T., Richards, D.R., 1999. Essential versus alternative foods of insect predators: benefits of a mixed diet. Oecologia 121, 107–112.
- Frazer, B.D., 1988. Coccinellidae. In: "Aphids-Their Biological, Natural Enemies and Control". A.K. Minks and P. Harrewijn (eds.), vol. B. Elsevier Science Publishers B.V., Amsterdam.
- Hodek, I., 1993. Habitat and food specificity in aphidophagous predators. Biocont. Sci. Technol. 3, 91–100.
- Hodek, I., Honěk, A., 1996. Ecology of Coccinellidae. Kluwer Academic Publishers., Netherlands.
- Honěk, I., Kocourek, F., 1990. Temperature and development time in insects: A general relationship between thermal constants. Zool. Jb. Syst. 117, 401–439.
- Ilharco, F.A., 1982. Afidofauna açoriana: comentários zoogeográficos (Homoptera, Aphidoidea). Bolm. Soc. Port. Ent. 7, 258–275.
- Işıkber, A.A., Copland, M.J.W., 2002. Effects of various aphid foods on *Cycloneda sanguinea*. Entomol. Exp. Appl. 102, 93–97.
- Kalushkov, P., 1998. Ten aphid species (Sternorrhyncha: Aphidae) as prey for *Adalia bipunctata* (Coleoptera: Coccinellidae). Eur. J. Entomol. 95, 343–349.
- Kalushkov, P., Hodek, I., 2001. New essential aphid prey for *Anatis ocellata* and *Calvia quatuordecimgottata* (Coleoptera: Coccinellidae). Biocont. Sci. Technol. 11, 35–39.
- Kalushkov, P., Hodek, I., 2004. The effects of thirteen species of aphids on some life history parameters of the ladybird *Coccinella septempunctata*. BioControl 49, 21–32 1984–1092.
- Krebs, C.J., 1994. Ecological Methodology. Harper Collins Publishers, New York, USA.
- Martin, N.A., 1999. Whitefly, Biology, Identification and Life cycle. New Zealand Institute, Auckland, N.Z.
- Michaud, J.P., 2005. On the assessment of prey suitability in aphidophagous Coccinellidae. Eur. J. Entomol. 102, 385–390.
- Minks, A.K., Harrewijn P., 1989. Aphids—Their Biological, Natural Enemies and Control., vol. C. Elsevier Science Publishers B.V., Amsterdam.
- Nijjima, K., Matsuka, M., Okada, I., 1986. Artificial diets for an aphidophagous coccinellid, *Harmonia axyridis*, and its nutrition (Minireview). Ecology of Aphidophaga. Academia, Prague.
- Nijjima, K., Takahashi, H., 1980. Nutritional studies of an aphidophagous coccinellid, *Harmonia axyridis* (IV). Effects of chemically defined diet and some fractions of drone honeybee on the reproduction. Bull. Fac. Agric. Tamagawa Univ. 20, 47–55.

- Obyrcki, J.J., Orr, C.J., 1990. Suitability of three prey species for Nearctic populations of *Coccinella septempunctata*, *Hippodamia variegata*, and *Propylea quatuordecimpunctata* (Coleoptera: Coccinellidae). *J. Econ. Entomol.* 4, 1292–1297.
- Olszak, R.W., 1988. Voracity and development of three species of Coccinellidae, preying upon different species of aphids. *Ecology and Effectiveness of Aphidophaga*, 47–53.
- Omkar, G.M., 2005. Preference-performance of generalist predatory ladybird: a laboratory study. *Biol. Control* 34, 187–195.
- Raimundo, A.A.C., Alves, L.L.G., 1986. Revisão dos coccinélidos em Portugal. Publicações da Universidade de Évora, Évora.
- Rana, J.S., Dixon, A.F.G., Jarosik, V., 2002. Costs and benefits of prey specialization in a generalist insect predator. *J. Anim. Ecol.* 71, 15–22.
- Shanderl, H., 1987. Détermination des conditions optimales d'élevages de la coccinelle *Harmonia axyridis* Pallas (Col., Coccinellidae), et possibilité d'une production continue à l'aide d'une proie de substitution, les oeufs d'*Ephestia kuehniella* Zeller (Lep., Pyralidae). PhD thesis, Université de Droit, d'Economie et des Sciences, d'Aix Marseille, Marseille.
- Soares, A.O., Coderre, D., Schanderl, H., 2004. Dietary self-selection behaviour by the adults of the aphidophagous ladybeetle *Harmonia axyridis* (Coleoptera: Coccinellidae). *J. Anim. Ecol.* 73, 478–486.
- Soares, A.O., Coderre, D., Schanderl, H., 2005. Influence of prey quality on the fitness of two phenotypes of *Harmonia axyridis* adults. *Entomol. Exp. Appl.* 114, 227–232.
- Southwood, T.R.E., Henderson, P.A., 2000. *Ecological Methods*. Blackwell Science, Oxford, UK.
- SPSS Inc, 2003. *SPSS Base 12.0 for Windows User's Guide*. Chicago, Illinois.
- Tsaganou, F.C., Hodgson, C.J., Athanassiou, C.G., Kavallieratos, N.G., Tomanović, Z., 2004. Effect of *Aphis gossypii* Glover, *Brevicoryne brassicae* (L.), and *Megoura viciae* Buckton (Hemiptera: Aphidoidea) on the development of the predator *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae). *Biol. Control* 31, 138–144.
- Zar, J.H., 1996. *Biostatistical Analysis*. Prentice-Hall, London, UK.
- Zaki, F.N., El-Shaarawy, M.F., Farag, N.A., 1999. Release of two predators and two parasitoids to control aphids and whiteflies. *J. Pest. Sci.* 72, 19–20.