

Does pirimicarb affect the voracity of the euriphagous predator, *Coccinella undecimpunctata* L. (Coleoptera: Coccinellidae)?

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Abstract

Pirimicarb is considered a selective and effective insecticide for the control of aphids and whiteflies. *Coccinella undecimpunctata* L. is a euriphagous predator autochthonous to the Azores, which feeds preferentially on aphids. The voracity of 4th instars and adults (males and females) of *C. undecimpunctata* using *Aphis fabae* Scopoli or *Aleyrodes proletella* L. as preys was evaluated in laboratory, as well as the impact of pirimicarb on the feeding performance using *A. fabae* as prey. In the absence of chemical treatment and when the prey was *A. proletella*, satiation lower limits were estimated on a density of 200 individuals in a 24-h period, for 4th instars, adult females and males of *C. undecimpunctata*. With *A. fabae*, satiation was attained when 200, 150 and 100 aphids were provided to 4th instars, adult females and males, respectively. *C. undecimpunctata* exhibited a type II functional response for both prey species. Fourth instars displayed a lower handling time than the adults; handling times of the adults were higher when *A. fabae* was the prey and attack rates were sex-dependent, that is, attack rate of females was higher on *A. fabae* while of males was higher on *A. proletella*. Voracity of *C. undecimpunctata* was not significantly affected by pirimicarb; therefore, the use of this insecticide can constitute a complementary component for the integrated management of *A. fabae*.

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1. Introduction

The damages that aphid and whitefly populations may cause in crop systems compel farmers to use insecticides as a way to guarantee an economically profitable production (Ilharco et al., 2004). Besides the development of pest resistance (Denholm et al., 2001), the extensive use of insecticides in crop systems surely has effects on non-target organisms. Among these effects, the reduction of the efficiency of biological control agents, such as coccinellid predators, has been highlighted by several authors (Hurej and Dutcher, 1994; Biddinger and Hull, 1995; Hamilton and Lashomb, 1997; Tillman and Mulrooney, 2000; Qi et al., 2001; Grafton-Cardwell and Gu, 2003; Youn et al., 2003; Liu and Stansly, 2004; Gal-

van et al., 2005). Insecticides may cause the death of the biological control agents (lethal effects) or change several other features of their biology, without killing the individuals (sub-lethal effects). Several insecticides have effects on the longevity and fecundity (Hamilton and Lashomb, 1997; Liu and Stansly, 2004; Galvan et al., 2005), developmental rates and sex ratios (Galvan et al., 2005), predation rates (Qi et al., 2001) and mobility (Provost et al., 2003) of Coccinellidae.

Pirimicarb, a dimethylcarbamate insecticide considered highly selective and safe to coccinellid predators (Amaro and Baggiolini, 1982; Jansen, 2000; James, 2003), is frequently used against aphids and whiteflies (Direção Geral de Proteção das Culturas, 2004; Syngenta, 2004). Integration of biological and chemical controls requires knowledge of the sub-lethal effects that insecticides may have on natural enemies, such as the effects on feeding performance. However, such effects

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are rarely evaluated despite the interest of understanding the feeding behavior of insect predators (Doubbia et al., 1998). Firstly, the comprehension of the interactions between predator and prey (such as voracity rates) allows us to evaluate the predator's potential as a biological control agent (ElHag and Zaitoon, 1996; Tsaganou et al., 2004). Second, the maximization of fitness and the increase of numerical reproductive response in lady beetles depend greatly on their ability to access and exploit prey patches (Kindlmann and Dixon, 1993). Thus, all the factors that disrupt the feeding performance of lady beetles will decrease their potential as biological control agents.

Coccinella undecimpunctata L. (Coleoptera: Coccinellidae) is a euriphagous predator that prefers to feed on aphids (Hodek and Honěk, 1996). This lady beetle is autochthonous for the Azores, Portugal, and has potential as a biological control agent against aphids and whiteflies (Soares et al., 2003b).

Aphis fabae Scopoli (Homoptera: Aphididae) and *Aleyrodes proletella* L. (Homoptera: Aleyrodidae) are considered two major pests in the agricultural systems of Azores causing serious damages in horticulture, both in fields and greenhouses. Since pests may be simultaneously present in the crops, farmers frequently use the insecticide pirimicarb. Despite the studies that report on the effects of pirimicarb on coccinellid predators (Garcia, 1979; James, 2003), the impact of this insecticide on the voracity has never been studied. In this study, we evaluated: (i) the voracity of 4th instars and adults (males and females) of *C. undecimpunctata* using *A. fabae* or *A. proletella* as preys; (ii) the response of *C. undecimpunctata* to prey density (i.e., the shape of the response curve); and (iii) the effect of pirimicarb on the voracity of *C. undecimpunctata* using *A. fabae* as prey.

2. Materials and methods

2.1. Insects

Coccinella undecimpunctata adults were collected in Sta. Maria Island, Azores, Portugal, early in the summer before experiments took place. Lady beetles were reared at 22 ± 1 °C, $75 \pm 5\%$ RH and a photoperiod of 16L:8D, using fluorescent lamps (Philips ref. TDL 23 W/54 and TDL 18 W/54). Insects were fed with an ad libitum supply of different developmental stages of aphids [*A. fabae* and *Myzus persicae* Sulzer (Homoptera: Aphididae)] and whiteflies (*A. proletella*) and, eggs of the Mediterranean flour moth, *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae). The mixed diet was provided to avoid food adaptation (Rana et al., 2002) and to supply a more widened group of nutrients to the predator. Colonies of *A. fabae* and *A. proletella* were, respectively, reared on *Vicia faba major* L. at 15 ± 1 °C and $75 \pm 5\%$ RH and on *Brassica oleracea* L. (var. *Costata*) at 25 ± 1 °C and $75 \pm 5\%$ RH. Photoperiod was of 16L:8D using fluores-

cent lamps (Philips ref. TDL 23 W/54 and TDL 18 W/54).

2.2. Voracity

Voracity of 4th instars and adults (males and females) was evaluated on single diets of *A. fabae* or *A. proletella*. Prior to the experiments, adults and larvae were held in separate Petri dishes (3 cm in depth and 5 cm in diameter) and fed ad libitum with the mixed diet. Larvae were maintained under these conditions until 24 h after molting to the 4th instar, while adults were kept until they became sexually mature (approximately 15 days after emergence).

Each individual of the 4th instars, female or male lady beetles was provided with one of the following prey densities: 5, 10, 20, 40, 80, 100, 200 or 300 nymphs of the 2nd and 3rd instars of *A. proletella*; and 5, 10, 20, 40, 80, 100, 150, 200 or 300 nymphs of the 3rd and 4th instars of *A. fabae*. After 24 h, the number of surviving preys was recorded in each treatment. All treatments were performed at 25 ± 1 °C, $75 \pm 5\%$ RH and a photoperiod of 16L:8D under fluorescent lamps (Sanyo FL 40 SS W/37). In order to evaluate the ratio of natural mortality of preys, control treatments were performed with the above-mentioned prey densities, but in the absence of predators. Abiotic conditions were the same as previously mentioned. Ten replicates for each treatment were performed.

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

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

where V_o is the number of eaten aphids or whiteflies, A is the number of aphids or whiteflies available, a_{24} is the number of aphids or whiteflies alive after 24 h and ra_{24} is the ratio of aphids or whiteflies alive after 24 h in the control treatment.

2.3. Functional response

Data were fit to the “random-predator” equation (Rogers, 1972), a modification of Holling's (1959) disk equation, regarded more appropriated because considers prey density to be affected by prey consumption (Hazzard and Ferro, 1991):

$$\frac{N_a}{TP} = \frac{\alpha N}{1 + \alpha T_h N}$$

where N_a is the number of preys attacked, T is the total time of prey exposure, P is the number of predators, N is the initial prey density, α is the attack rate (or searching efficiency) and T_h is the handling time (i.e., the time spent handling each prey attacked). In this experiment, $T = P = 1$, because preys were exposed to one predator for 1 day. The parameters α and T_h were estimated using two dependent variables: (i) number of aphids consumed and (ii) number of whiteflies consumed.

2.4. Insecticide treatment

In this experiment, the influence of pirimicarb on the voracity of *C. undecimpunctata* (4th instars and adult males and females) was evaluated on a single diet of *A. fabae*. Pirimicarb (Pirimor G, WG [0.375 kg (AI)/ha], Syngenta) was applied at the field rate recommended by the manufacturer for the control of aphids. Prior to the insecticide treatments, adults and larvae were held in separate Petri dishes (3 cm in depth and 5 cm in diameter) and fed ad libitum with the mixed diet. Fourth instars and adults were treated 24 h after molting and 15 days after emergence, respectively. Lady beetles were treated using a Potter Precision Spray Tower (Burkard, Rickmansworth, UK), calibrated at 2 kPa to deliver a homogenous spray coverage (1000 l/ha). Controls were sprayed only with distilled water. Previous to each treatment, lady beetles were placed into plastic Petri dish bottoms (150 × 15 mm) and held during 30 min at 15 °C to diminish the insect mobility. After spraying, insects were allowed to dry for 1 h before their transference to separate untreated Petri dishes (3 cm in depth and 5 cm in diameter) containing *A. fabae* (nymphs of the 3rd and 4th instars). In this experiment, the selected number of preys per predator corresponded to the minimum necessary to satiate the matching developmental instars of the predator, previously determined in the voracity tests. Voracity of *C. undecimpunctata* was evaluated 24 h after the first contact with the prey and analyzed as described above. Ten individuals of each studied developmental instars of *C. undecimpunctata* were treated. All treatments were performed at 25 ± 1 °C, 75 ± 5% RH and a photoperiod of 16L:8D under fluorescent lamps (Sanyo FL 40 SS W/37).

2.5. Statistical analysis

Voracity data were compared by one-factor ANOVA. When ANOVA showed significant differences ($P < 0.05$) among data sets, paired comparisons of each mean were made using Fisher's protected LSD tests (Zar, 1996). All analyses were performed using SPSS v. 12.0 for Windows (SPSS, Inc., 2004).

Functional response model parameters were calculated and the curve was plotted for untransformed data, using the nonlinear regression module of SPSS v. 12.0 for Windows (SPSS, Inc., 2004). Significance of the regression models was evaluated by ANOVA and the variance explained by the model was expressed by the coefficient of determination.

3. Results

3.1. Voracity

For both prey species, the number of preys eaten by 4th instars of *C. undecimpunctata* increased significantly with prey density ($F_{(8,90)} = 56.98$, $P \leq 0.0001$, for *A. fabae*; $F_{(7,82)} = 22.82$, $P \leq 0.0001$, for *A. proletoella*), reaching the maximum value when 200 preys were provided (i.e.,

80.24 ± 6.12 and 80.83 ± 12.07 preys were consumed for *A. fabae* and *A. proletoella*, respectively). Female's voracity also increased significantly with prey density ($F_{(8,140)} = 38.13$, $P \leq 0.0001$, for *A. fabae*; $F_{(7,80)} = 22.19$, $P \leq 0.0001$, for *A. proletoella*), reaching the maximum value when 150 preys were provided (i.e., 40.01 ± 5.02 and 56.84 ± 7.41 preys were consumed for *A. fabae* and *A. proletoella*, respectively). Similarly, male's voracity increased significantly with the number of preys provided ($F_{(7,80)} = 55.36$, $P \leq 0.0001$, for *A. fabae*; $F_{(7,80)} = 20.99$, $P \leq 0.0001$, for *A. proletoella*), but satiation was attained at a lower density when the prey was *A. fabae*, that is, when 100 aphids were provided per male (i.e., 37.83 ± 2.65 and 60.26 ± 7.81 preys were consumed for *A. fabae* and *A. proletoella*, respectively; Tables 1 and 2).

3.2. Functional response

Voracity data fitted to the modified Holling disk equation showed that the number of preys consumed and the amount of ingested biomass during 24 h increased with prey density at a monotonic decelerating rate, representing a typical type II response (Figs. 1 and 2). Estimated models

Table 1

Voracity (mean number of preys eaten ± SE) of *C. undecimpunctata* 4th instars and adults (females and males) fed on different densities of *A. fabae*

Prey density (number of preys provided)	Voracity ± SE		
	Larvae (4th instars)	Adult females	Adult males
5	3.80 ± 0.55a	4.14 ± 0.08a	4.29 ± 0.42a
10	9.36 ± 0.39ab	8.28 ± 0.08ab	5.27 ± 0.77a
20	19.31 ± 0.19bc	13.95 ± 0.69bc	7.41 ± 0.72a
40	24.38 ± 0.76c	20.20 ± 1.43c	17.29 ± 1.61b
80	36.10 ± 1.82d	29.94 ± 1.94d	28.75 ± 3.68c
100	41.54 ± 3.52d	31.29 ± 7.55de	37.83 ± 2.65d
150	53.13 ± 1.60e	40.01 ± 5.02ef	42.27 ± 2.02d
200	80.24 ± 6.12f	40.31 ± 2.80f	40.46 ± 3.16d
300	90.68 ± 9.34f	43.70 ± 2.51f	—

Means within a column followed by different letters are significantly different at $P < 0.05$ (LSD test).

Table 2

Voracity (mean number of preys eaten ± SE) of *C. undecimpunctata* 4th instars and adults (females and males) fed on different densities of *A. proletoella*

Prey density (number of preys provided)	Voracity ± SE		
	Larvae (4th instars)	Adult females	Adult males
5	1.85 ± 0.49a	2.83 ± 0.59a	3.02 ± 0.55a
10	2.63 ± 0.39a	4.68 ± 1.33a	7.70 ± 0.73a
20	8.87 ± 1.47ab	11.02 ± 1.99a	12.58 ± 2.03a
40	24.37 ± 2.22bc	15.11 ± 3.82a	27.59 ± 2.28a
80	39.35 ± 6.68cd	38.91 ± 4.28b	42.41 ± 5.26c
100	43.48 ± 4.81d	43.87 ± 7.69b	43.68 ± 7.89cd
200	80.83 ± 12.07e	56.84 ± 7.41c	60.26 ± 7.81de
300	79.27 ± 11.93e	66.79 ± 6.89c	65.02 ± 7.35e

Means within a column followed by different letters are significantly different at $P < 0.05$ (LSD test).

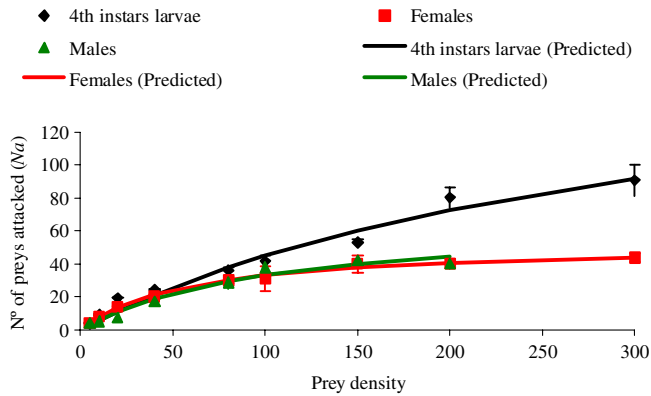


Fig. 1. Functional response of *C. undecimpunctata* 4th instars and adults (females and males) fed on different prey densities of *A. fabae* during 24 h. Models of “random-predator” equation (Rogers, 1972) were calculated and plotted for untransformed data, using the nonlinear regression module of SPSS, v. 12.0.

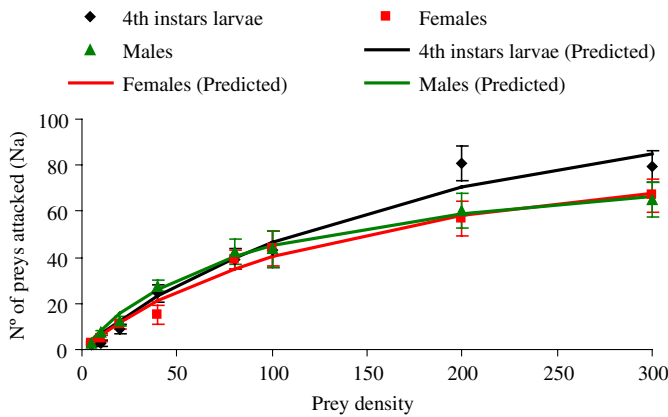


Fig. 2. Functional response of *C. undecimpunctata* 4th instars and adults (females and males) fed on different prey densities of *A. proleptella* during 24 h. Models of “random-predator” equation (Rogers, 1972) were calculated and plotted for untransformed data, using the nonlinear regression module of SPSS, v. 12.0.

accounted for a significant portion of the initial variance of the data for voracity of 4th instars, female and male of the lady beetle (Tables 3 and 4).

Results showed that (i) 4th instars displayed a lower handling time (T_h) than adults, (ii) handling times of the adults on *A. fabae* were higher than on *A. proleptella* and (iii) attack rates (α) were sex-dependent, that is, attack rate of females was higher on *A. fabae* while of males was higher on *A. proleptella* (Tables 3 and 4).

Table 3

Attack rate (α) and handling time (T_h) estimated by the modified Holling disk equation, and respective standard errors (SE) and 95% confidence intervals, for the 4th instars and adults (females and males) of *C. undecimpunctata* fed on *A. fabae*

	Parameters	Estimate	Asymptote (SE)	95% CI		
				Lower	Upper	
Larvae (4th instars)	α	0.592	0.062	0.468	0.715	$F_{(2,90)} = 56.98, P < 0.05, R^2 = 0.82$
	T_h	0.005	0.0008	0.004	0.007	
Adult females	α	0.906	0.129	0.651	1.161	$F_{(2,140)} = 38.13, P < 0.05, R^2 = 0.70$
	T_h	0.019	0.001	0.017	0.021	
Adult males	α	0.649	0.085	0.48	0.819	$F_{(2,80)} = 55.36, P < 0.05, R^2 = 0.82$
	T_h	0.015	0.002	0.012	0.018	

3.3. Insecticide treatment

Results showed that the voracity of *C. undecimpunctata* was not significantly affected by pirimicarb treatments ($F_{(1,19)} = 0.050, P = 0.826$) for 4th instars; ($F_{(1,29)} = 0.158, P = 0.694$ for females; $F_{(1,19)} = 1.57, P = 0.226$ for males), when the provided number of preys corresponded to the density of the predator’s maximum voracity (Fig. 3).

4. Discussion

Our results showed that *C. undecimpunctata* was able to eat a large amount of individuals of *A. fabae* and *A. proleptella*, mainly for densities beyond 100 preys. For *A. proleptella*, full satiation jointly with high levels of predation was estimated on a prey density of 200 individuals, regardless of the predator’s developmental stage. When the prey was *A. fabae*, satiation was attained on prey density of 200, 150 and 100 aphids to 4th instars, females and males, respectively. These results suggest a great ability of *C. undecimpunctata* to exploit patches where these preys would be present and, thus, could be used for the biological control of both prey species. Regarding the higher voracity of the adults on *A. proleptella* than on *A. fabae*, it seems that this predator should be a useful biological control agent to use in an inoculation strategy against the former species. However, more experiments should be performed to access the predator’s survival, reproductive performance and ability to display feeding preferences for the preys used in the experiments. These results will be important to foresee the ability of *C. undecimpunctata* to assess patches quality in terms of their potential to sustain the development of their larvae.

It is noteworthy that voracity of females and males did not differ, when the preys were either *A. fabae* or *A. proleptella*. Indeed functional response curves for both sexes, in Figs. 1 and 2, are overlapped. Generally, the predators’ size is positively correlated to mean prey size and capture success decreases with increasing prey size (Pastorok, 1981; Malcolm, 1992; Sabelis, 1992; Roger et al., 2000; Soares et al., 2001, 2003a). Thus, due to their small size, males would be more prone to eat small preys to become satiated (Dixon, 2000; Soares et al., 2004). However, the absence of differences in voracities could be explained by the fact of having used different instars of nymphs with different body sizes (i.e., nymphs of the 3rd and 4th instars of aphids and

Table 4

Attack rate (α) and handling time (T_h) estimated by the modified Holling disk equation and, respective standard errors (SE) and 95% confidence intervals, for the 4th instars and adults (females and males) of *C. undecimpunctata* fed on *A. prolella*

	Parameters	Estimate	Asymptote (SE)	95% CI		
				Lower	Upper	
Larvae (4th instars)	α	0.687	0.128	0.432	0.942	$F_{(2,82)} = 22.28, P < 0.05, R^2 = 0.66$
	T_h	0.006	0.001	0.004	0.009	
Adult females	α	0.673	0.124	0.425	0.92	$F_{(2,80)} = 22.94, P < 0.05, R^2 = 0.67$
	T_h	0.01	0.002	0.007	0.013	
Adult males	α	0.938	0.172	0.595	1.281	$F_{(2,80)} = 20.99, P < 0.05, R^2 = 0.67$
	T_h	0.012	0.001	0.009	0.014	

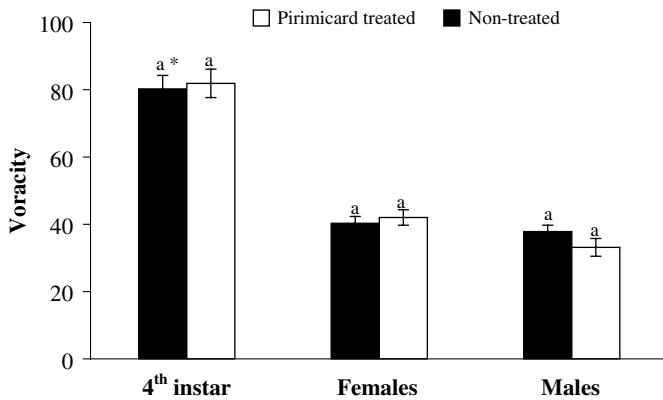


Fig. 3. Voracity of *C. undecimpunctata* 4th instars and adults (females and males) treated and non-treated with pirimicarb, using *A. fabae* as preys. *Means in each column for each developmental instars followed by different letters are significantly different at $P < 0.05$ (LSD test).

2nd and 3rd instars of whiteflies) and males may have consumed the smaller individuals, thus increasing their voracity. In fact, recent results from Soares et al. (2004) highlight that males of *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae), under mixed diets of different preys, display a preference for the smaller preys.

The functional response characterizes a relation between the attack rate by a predator and its prey density. The relationship may be represented by a constant (density-independent curve, type I), a decreasing curve (decelerating density dependence, type II) or increasing curve (density-dependent over a limited range of prey densities, type III) (Holling, 1959). *Coccinella undecimpunctata* exhibited a type II functional response for both prey species, i.e., a convex curve that represents a decelerating increase in the number of consumed preys with increasing prey density (Ferran and Dixon, 1993). From the practical point of view, this type of response implies that *C. undecimpunctata* can be considered a good agent for the biological control of aphids and whiteflies.

According to the model, the number of attacked prey items increases with the total time, prey density and/or attack rate, but decreases as handling time increases (Holling, 1959). Handling time includes time spent pursuing, subduing and consuming each prey item, plus the time spent preparing to search for the next prey (including effects of satiation) (Mills, 1982). Results show that (i) 4th

instars displayed a lower handling time (T_h) than adults, (ii) handling times of the adults on *A. fabae* were higher than on *A. prolella* and (iii) attack rate (α) of females were higher on *A. fabae* while of males were higher on *A. prolella* (Tables 3 and 4). Three main factors could explain these results: higher foraging activity of larvae (which led a decrease of handling time), differences between size of *A. fabae* and *A. prolella*, and/or preference of *C. undecimpunctata* for aphids. Indeed nymphs of *A. fabae* are bigger than that of *A. prolella* and, according to Hodek and Honěk (1996), *C. undecimpunctata* prefers to eat on aphids. Therefore, it seems that females of *C. undecimpunctata*, contrarily to males, more rapidly generate a success attack after an encounter with the suitable *A. fabae* than with *A. prolella*, despite the higher ability of aphids in escape responses. In fact, a recent study indicates that female lady beetles (*H. axyridis*) are more selective in what prey quality is concerned (Soares et al., 2004). Our results also showed that the contact between females and whiteflies probably stimulates an intensive search for better preys and that males more rapidly consume the smallest whiteflies than the larger aphids.

Voracity of *C. undecimpunctata* was not significantly affected by pirimicarb treatments. Garcia (1979) also observed that of 4th instars of *Cheilomenes sulphurea* and *Semidalia undecimnotata* (Coleoptera: Coccinellidae) continue to feed after pirimicarb treatments. According to Jansen (2000) and James (2003), this insecticide is highly selective, being considered safe for some species of Coccinellidae. However, Schmuck et al. (1997) observed that the fecundity of *C. septempunctata* was affected by the insecticide treatments. Similarly, Olszak (1999) observed that the fecundity of *Adalia bipunctata* L. (Coleoptera: Coccinellidae) decreased following the insecticide treatments.

Since the voracity was not affected by pirimicarb, a combination of *C. undecimpunctata* with this selective insecticide may be considered in the implementation of aphid control programs. Nevertheless, other sub-lethal effects, such as the reduction of coccinellid fecundity, observed in other species (Schmuck et al., 1997; Olszak, 1999) must not be disregarded. Therefore, further studies focusing on the effects of pirimicarb on reproductive parameters of *C. undecimpunctata* need to be performed.

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References

- Amaro, P., Baggiolini, M., 1982. In: Introdução à protecção integrada, vol. I. FAO/DGPPA, Lisboa.
- Biddinger, D.J., Hull, L.A., 1995. Effects of several types of insecticides on the mite predator, *Stethorus punctum* (Coleoptera: Coccinellidae), including insect growth regulators and abamectin. *J. Econ. Entomol.* 88, 358–366.
- Denholm, I., Pickett, J.A., Devonshire, A.L., 2001. Insecticide Resistance: From Mechanisms to Management. CABI and The Royal Society publishing, London, UK.
- Direcção Geral de Protecção das Culturas, 2004. Lista de protecção integrada de Hortícolas. S. Miguel, Açores.
- Dixon, A.F.G., 2000. Insect Predator–Prey Dynamics. Cambridge University Press, London.
- Doumbia, A., Hemptinne, J.-L., Dixon, A.F.G., 1998. Assessment of patch quality by ladybirds: role of larval tracks. *Oecologia* 113, 197–202.
- ElHag, E.T.A., Zaitoon, A.A., 1996. Biological parameters for four coccinellid species in central Saudi Arabia. *Biol. Control* 7, 316–319.
- Ferran, A., Dixon, A.F.G., 1993. Foraging behaviour of ladybird larvae (Coleoptera: Coccinellidae). *Eur. J. Entomol.* 90, 383–402.
- Galvan, T.L., Koch, R.L., Hutchinson, W.D., 2005. Effects of spinosad and indoxacarb on survival, development and reproduction of the multicoloured Asian lady beetle (Coleoptera: Coccinellidae). *Biol. Control* 34, 108–114.
- Garcia, V., 1979. Efeitos de um aficida sobre as potencialidades biológicas de dois predadores afídi fagos: *Cheilomenes sulphurea* (Olivier) e *Semidalia undecimnotata* Schneider (Coleoptera: Coccinellidae). Ph.D. Thesis. University of Azores, Ponta Delgada, Portugal.
- Grafton-Cardwell, E., Gu, P., 2003. Conserving vedalia beetle, *Rodolia cardinalis* (Mulsant) (Coleoptera: Coccinellidae), in citrus: a continuing challenge as new insecticides gain registration. *J. Econ. Entomol.* 96, 1388–1398.
- Hamilton, G.C., Lashomb, J.H., 1997. Effect of insecticides on two predators of the Colorado potato beetle (Coleoptera: Chrysomelidae). *Fla. Entomol.* 80, 10–23.
- Hazzard, R.V., Ferro, D.N., 1991. Feeding responses of adults *Coleomegilla maculata* (Coleoptera: Coccinellidae) to eggs of Colorado potato beetle (Coleoptera: Chrysomelidae) and green peach aphids (Homoptera: Aphididae). *Environ. Entomol.* 20, 644–651.
- Hodek, I., Honěk, A., 1996. Ecology of Coccinellidae. Kluwer Academic Publishers, The Netherlands.
- Holling, C.S., 1959. Some characteristics of simple types of predation and parasitism. *Can. Entomol.* 91, 385–398.
- Hurej, M., Dutcher, J.D., 1994. Indirect effect of insecticides on convergent lady beetle (Coleoptera: Coccinellidae) in Pecan Orchards. *J. Econ. Entomol.* 87, 1632–1635.
- Ilharco, F.A., Valério, E., Cecílio, A., Mexia, A., 2004. Dinâmica das populações de afídeos (Homoptera: Aphidoidea) e os seus parasitóides (Hymenoptera: Aphididae) em cultura protegida de pimento. Fundação Callouste Gulbenkian, Lisboa, Portugal.
- James, D.G., 2003. Pesticide susceptibility of two coccinellids (*Stethorus punctum picipes* and *Harmonia axyridis*) important in biological control of mites and aphids in Washington Hops. *Biocont. Sci. Tech.* 13, 253–259.
- Jansen, J.P., 2000. A three-year field study on short term effects of insecticides used to control cereal aphids on plant-dwelling aphid predators in winter wheat. *Pest Manag. Sci.* 56, 533–539.
- Kindlmann, P., Dixon, A.F.G., 1993. Optimal foraging in ladybird beetles (Coleoptera: Coccinellidae) and its consequences for their use in biological control. *Eur. J. Entomol.* 90, 443–450.
- Liu, T.-X., Stansly, P.A., 2004. Lethal and sublethal effects of two insect growth regulators on adult *Delphastus catalinae* (Coleoptera: Coccinellidae), a predator of whiteflies (Homoptera: Aleyrodidae). *Biol. Control* 30, 298–305.
- Malcolm, S.B., 1992. Prey defence and predator foraging. In: Crawley, M.J. (Ed.), *Natural Enemies*. Blackwell Scientific Publications, Oxford, pp. 458–475.
- Mills, N.J., 1982. Satiation and the functional response: a test of a new model. *Ecol. Entomol.* 7, 305–315.
- Olszak, R.W., 1999. Influence of some pesticides on mortality and fecundity of the aphidophagous coccinellid *Adalia bipunctata* L. (Col., Coccinellidae). *J. Appl. Ent.* 123, 41–45.
- Pastorok, R.A., 1981. Prey vulnerability and size selection by chaoborus larvae. *Ecology* 62, 1311–1324.
- Provost, C., Coderre, D., Lucas, E., Bostanian, N.J., 2003. Impact of lambda-cyhalothrin on intraguild predation among three mite predators. *Environ. Entomol.* 32, 256–263.
- Qi, B., Gordon, G., Gimne, W., 2001. Effects of neem-fed prey on the predacious insects *Harmonia conformis* (Boisduval) (Coleoptera: Coccinellidae) and *Mallada signatus* (Schneider) (Neuroptera: Chrysopidae). *Biol. Control* 22, 185–190.
- 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.
- Roger, C., Coderre, D., Boivin, G., 2000. Differential prey utilization by generalist predator *Coleomegilla maculata* lengi according to prey size and species. *Entomol. Exp. Appl.* 94, 3–13.
- Rogers, D.J., 1972. Random search and insect population models. *J. Anim. Ecol.* 41, 369–383.
- Sabelis, M.W., 1992. Predatory arthropods. In: Crawley, M.J. (Ed.), *Natural Enemies*. Blackwell Scientific Publications, Oxford, pp. 225–264.
- Schmuck, R., Tornier, I., Bock, K.D., Waltersdorfer, A., Kunast, Ch., 1997. A semi-field testing procedure using the ladybird beetle, *Coccinella septempunctata* L. (Col., Coccinellidae), for assessing the effects of pesticides on non-target leaf-dwelling insects under field exposure conditions. *J. Appl. Ent.* 121, 111–120.
- Soares, A.O., Coderre, D., Schanderl, H., 2001. Influence of phenotype on fitness parameters of *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae). *Eur. J. Entomol.* 98, 287–293.
- Soares, A.O., Coderre, D., Schanderl, H., 2003a. Effect of temperature and intraspecific allometry on predation by two phenotypes of *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae). *Env. Entomol.* 32, 939–944.
- Soares, A.O., Elias, R.B., Resendes, R., Figueiredo, H., 2003b. Contribution to the knowledge of the Coccinellidae (Coleoptera) fauna from the Azores islands. *Arquipélago, Life Mar. Sci.* 20, 47–53.
- 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.
- SPSS, Inc., 2004. SPSS Base 12.0 for Windows User's Guide. SPSS, Inc., Chicago, IL, USA.
- Syngenta, 2004. Catálogo. Syngenta Crop Protection. Syngenta, Lisboa/Portugal.
- Tillman, P.G., Mulrooney, J.E., 2000. Effect of selected insecticides on the natural enemies *Colleomegilla maculata* and *Hippodamia convergens* (Coleoptera: Coccinellidae), *Geocoris punctipes* (Hemiptera: Lygaeidae), and *Bracon mellitor*, *Cardiochiles nigriceps*, and *Cotesia marginiventris* (Hymenoptera: Braconidae) in cotton. *J. Econ. Entomol.* 93, 1638–1643.
- 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.
- Youn, Y.N., Seo, M.J., Shin, J.G., Jang, C., Yu, Y.M., 2003. Toxicity of greenhouse pesticides to multicoloured Asian lady beetles, *Harmonia axyridis* (Coleoptera: Coccinellidae). *Biol. Control* 28, 164–170.
- Zar, J.H., 1996. Biostatistical Analysis. Prentice-Hall, London, UK.