

# Interference competition between ladybird beetle adults (Coleoptera: Coccinellidae): effects on growth and reproductive capacity

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**Abstract** Cage experiments were used to determine the minimum number of *Aphis fabae* Scopoli that females of the Azorean native ladybird beetle *Coccinella undecimpunctata* L. require per day to achieve maximum fecundity and to assess the effects of interference competition from conspecific and heterospecific [*Harmonia axyridis* (Pallas)] adult ladybirds on its growth and reproduction. The number of *A. fabae* at which females of *C. undecimpunctata* ate most aphids, achieved maximum reproduction and maintained their body weight, was 200. The presence of *H. axyridis* adults, unlike the presence of *C. undecimpunctata*, significantly affected the reproductive numerical response of *C. undecimpunctata* even though the resource was not in short supply. The results suggest that interference competition with heterospecifics may adversely affect the reproductive capacity of *C. undecimpunctata*. Based on previous results and those reported here, we suggest that the introduction of *H. axyridis* could endanger the population abundance and/or result in the competitive displacement of *C. undecimpunctata* from the Azorean ecosystem.

**Keywords** Coccinellidae · *Coccinella undecimpunctata* · *Harmonia axyridis* · Growth · Reproductive capacity · Interference competition

## Introduction

A number of studies have revealed that invading species have a negative impact on native species. Invading species may affect the dynamics and composition of guilds of established species, as the invaders may interact with established species, directly or indirectly, including through intraguild predation (IGP) (Obrycki et al. 1998; Lucas et al. 2002; Evans 2004). However, it is still poorly understood how introduced species reduce the fitness of the natives.

The invasive ladybird beetle *Harmonia axyridis* became dominant and replaced another exotic species, *Coccinella septempunctata* L., in the midwestern, Pacific Northwest and eastern states of the USA (Horn 1996; LaMana and Miller 1996; Brown and Miller 1998), which previously had caused significant changes in the structure of native coccinellid communities in alfalfa, corn and small grain fields in North America (Elliott et al. 1996; Evans 2004). *H. axyridis* apparently affected native arboreal lady beetle species [*Brachiacantha ursina* (F.), *Cycloneda munda* (Say) and *Chilocorus stigma* (Say)] in agricultural landscapes in south-western Michigan (Colunga-Garcia and Gage 1998). In its native range, *H. axyridis* is dominant and replaces *C. septempunctata* in northern Japan when aphids become scarce (Yasuda and Shinya 1997). Competitive displacement of *Cycloneda sanguinea* (L.) from citrus ecosystems in Florida by *H. axyridis* has been reported (Michaud 2002). The aggressive behavior of *H. axyridis* larvae possibly accounts for these replacements (Yasuda et al. 2001; Agarwala et al. 2003). Recent results, however, indicate that

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*H. axyridis* may not negatively affect the survival and food intake of the native *Coleomegilla maculata* De Geer (Hoogendoorn and Heimpel 2004).

*C. undecimpunctata* L. is one of the most important native aphidophagous predators in the Azores. It can be found mostly by the sea (salt lands) on plants where it may feed also on flower pollen (Félix and Soares 2004). The Palearctic species *H. axyridis* (Iablokoff-Khnzorian 1982) has not yet been introduced into the Azores. This euryphagous predator prefers aphids (Soares et al. 2001) but can feed on psyllids (Fye 1981; Michaud 2002), coccids (McLure 1987), spider mites (Lucas et al. 1997), immature stages of Lepidoptera, including eggs (Schanderl et al. 1988) and Coleoptera (Kalaskar and Evans 2001). If introduced into the Azores, it is likely that *H. axyridis* would compete for the same resources of *C. undecimpunctata*.

Recent studies of the magnitude, direction and symmetry of IGP between the different developmental stages of *H. axyridis* and *C. undecimpunctata* revealed that *H. axyridis* was most often the IG predator (Félix and Soares 2004). Although there is no IGP between adults of the two species, they may interact negatively by interfering with each other's foraging and oviposition (Lucas et al. 2002; Agarwala et al. 2003). Competition may occur indirectly when two or more lady beetles use the same resource, which is in short supply. This process is called exploitative competition. Competition may also occur through more direct interactions. It occurs when the organisms seeking a resource harm one other, even when the resource is not in short supply. This is called interference competition. If we assume that ladybird beetles expend some time and/or matter and/or energy on competition or the avoidance of competition, then there is less of those resources available for maintenance and reproduction (Krebs 1989).

The aims of this study were to determine (1) the minimum number of *Aphis fabae* Scopoli that females of *C. undecimpunctata* need per day to maximize their fecundity; (2) the effect of the presence of the adults of conspecifics and the heterospecific *H. axyridis* on the growth and reproductive capacity of *C. undecimpunctata* females; and (3) the potential impact of the exotic *H. axyridis*, through interference competition, on the fitness of *C. undecimpunctata*. We predict that the presence of both heterospecifics and conspecifics should adversely affect the fitness of *C. undecimpunctata*, when food is not in short supply, and possibly more so in the presence of *H. axyridis*, which does not occur in the Azores.

## Materials and methods

### Study organisms

*H. axyridis* and *C. undecimpunctata* adults came from stock cultures, which were reared at  $22 \pm 1^\circ\text{C}$ , with  $75 \pm 5\%$  RH and a photoperiod of L16:D8, using fluorescent lamps (Philips ref.: TDL 23W/54 and TDL 18W/54). In order to avoid consanguinity and food adaptation (Rana et al. 2002), ladybird beetles were fed *ad libitum* on a mixed diet of the aphids *A. fabae* Scopoli and *Myzus persicae* (Sulzer) plus eggs of *Ephestia kuehniella* Zeller, and field-collected lady beetles were added regularly to the stock culture. In the case of *H. axyridis*, an average of 200 field-collected individuals from Canada was added to the stock culture at least once a year.

Biological features of *C. undecimpunctata* females provided with different numbers of *A. fabae*

The number of apterous females of *A. fabae* eaten in 24 h by females of *C. undecimpunctata* was determined. There were seven treatments in which 1, 5, 10, 20, 100, 200 or 300 individuals of *A. fabae* were provided to ovipositing females. Females were 15 days old, approximately half of their expected longevity. Twenty replicates were conducted per treatment. All experiments were done at  $25 \pm 1^\circ\text{C}$ ,  $75 \pm 5\%$  RH and a photoperiod of L16:D8 under fluorescent lamps. The aphids were presented to a single female in a 2-l transparent plastic box containing a potted broad bean plant (approximately 15 cm in height). The aphids were replaced daily for 3 days on the same broad bean plant. Each set of aphids was weighed before being presented to the predators. Body weight of aphids and ladybirds was measured using a  $10^{-4}$ -mg Mettler AM 50 analytical balance. The females' voracity and reproductive capacity (measured as number of eggs laid per female per day, number of eggs laid per clutch per female per day and number of clutches laid per female per day) were recorded over the final 24 h of the 3-day experimental period. The increase in female body weight was estimated over the 72-h experimental period. Voracity ( $V_o$ ) was calculated according to the following model (Soares et al. 2003):

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

where  $V_o$  = number of aphids eaten,  $A$  = number of aphids provided,  $a_{24}$  = number of aphids alive after 24 h, and  $ra_{24}$  = survival of aphids after 24 h in the absence of the predator. Aphid survival in the absence

of a predator was determined at three prey densities (20, 200 and 300 aphids) using the same experimental setup. Ten replicates for each prey density were performed. Another measure of voracity is the biomass of prey ingested (mg) per unit of time, the so-called relative consumption rate (*RCR*). *RCR* was evaluated according to Soares et al. (2004):

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

where  $RCR_{(mg)}$  = relative consumption rate,  $W_i$  = total weight of aphids provided,  $N$  = number of aphids provided,  $V_o$  = number of aphids eaten and  $PUC$  = prey utilization coefficient. In a separate experiment, the *PUC* of *C. undecimpunctata* females was estimated to be  $72.6 \pm 2.8\%$  using the following model (Schanderl 1987)

$$PUC = [(W_0 - W_1 - (W'_0 - W'_1) / 2) / W_0] \times 100$$

where  $W_0$  = body weight of one aphid provided,  $W_1$  = aphid carcass weight,  $W'_0$  = initial body-weight and  $W'_1$  = final body weight of one aphid in the control treatment. One-factor ANOVA followed by a multiple comparison test (LSD test) was used to compare voracity, relative consumption rate, body-weight variation and reproductive capacity (SPSS Inc., 2003).

**Impact of the presence of conspecific and heterospecific adults on the growth and reproductive capacity of *C. undecimpunctata* females**

In this experiment, one female of *C. undecimpunctata* was kept for 3 days in the experimental set up (as previously described) and provided with 200 aphids per day. At the end of the second day, one conspecific (treatment 1) or one heterospecific (treatment 2) beetle was also released in the experimental setup. All the adults used in this experiment were reared under the same conditions and were the same age. On the third day, body weight and reproductive capacity of *C. undecimpunctata* females were recorded. In the replicates with two females of *C. undecimpunctata*, results for reproductive capacity were compared and presented per female. Twenty replicates (ten females and ten males) per treatment were conducted. The experiments were done at  $25 \pm 1^\circ\text{C}$ ,  $75 \pm 5\%$  RH and a photoperiod of L16:D8 under fluorescent lamps. Two-factor ANOVA was used to compare the mean changes in body weight, mean number of eggs laid, mean number of eggs laid per clutch per female and mean number of clutches laid per female kept alone, with a conspecific or a heterospecific.

## Results

**Biological features of *C. undecimpunctata* females provided with different numbers of *A. fabae***

The number of aphids eaten (ANOVA,  $F = 129.96$ ,  $df = 6$ ,  $139$ ,  $P \leq 0.0001$ ) and biomass ingested (ANOVA,  $F = 108.14$ ,  $df = 6$ ,  $P \leq 0.0001$ ) by *C. undecimpunctata* females in 24 h increased and reached maximum values when 200 aphids were provided (Table 1).

Changes in the body weight of *C. undecimpunctata* females over the 72-h experimental period differed significantly between treatments (ANOVA,  $F = 24.63$ ,  $df = 6$ ,  $139$ ,  $P \leq 0.0001$ ) (Fig. 1). Female body weight decreased significantly over the 3-day period when less than 100 aphids were provided. Body weight decreased substantially at feeding rates of 1, 5 and 10 aphids per day (among which no significant differences were observed). Less-severe decreases in body weight were observed when 20 or 100 aphids were provided. When 200 or 300 aphids were provided, an increase in body weight was observed (Fig. 1).

Fecundity differed significantly with treatment (ANOVA,  $F = 9.97$ ,  $df = 6$ ,  $P \leq 0.0001$ ) (Fig. 2A). The number of eggs increased and then levelled off at numbers of aphids provided greater than 20 (Fig. 2A).

Mean clutch size differed significantly with treatment (ANOVA,  $F = 12.1$ ,  $df = 6$ ,  $P \leq 0.0001$ ) (Fig. 2B). Clutch size increased up to and was greatest when 200 aphids were provided (Fig. 2B). A reduction in clutch size was noted at the feeding rate of 300 aphids (Fig. 2B).

The number of clutches differed significantly with treatment (ANOVA,  $F = 9.82$ ,  $df = 6$ ,  $P \leq 0.0001$ ) (Fig. 2C). Clutch number increased and then levelled off at numbers of aphids provided greater than 20 (Fig. 2C).

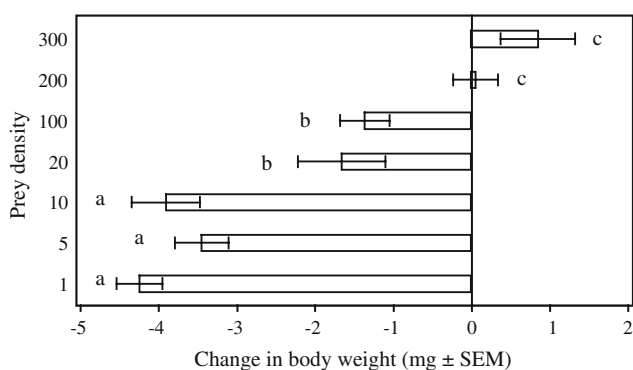
**Impact of the presence of conspecific and heterospecific adults on the growth and reproductive capacity of *C. undecimpunctata* females**

No significant differences were recorded in the body weights of *C. undecimpunctata* kept on their own or with conspecifics (ANOVA,  $F = 1.514$ ,  $df = 37$ ,  $P = 0.226$ ; Fig. 3A) or heterospecifics (ANOVA,  $F = 0.066$ ,  $df = 38$ ,  $P = 0.799$ ; Fig. 3B). Changes in body weight of *C. undecimpunctata* females did not differ according to the gender of conspecifics (ANOVA,  $F = 0.743$ ,  $df = 36$ ,  $P = 0.483$ ; Fig. 3A) or heterospecifics (ANOVA,  $F = 0.29$ ,  $df = 37$ ,  $P = 0.749$ ;

**Table 1** Mean voracity (mean number of aphids eaten  $\pm$  SE) and relative consumption rate (milligrams of biomass ingested  $\pm$  SE) of *Coccinella undecimpunctata* female, provided with different numbers of *Aphis fabae*

Number of aphids provided	Voracity <sup>a</sup>	Relative consumption rate
1	0.85 $\pm$ 0.00a	0.49 $\pm$ 0.02a
5	4.14 $\pm$ 0.08ab	2.26 $\pm$ 0.10ab
10	8.28 $\pm$ 0.08b	4.64 $\pm$ 0.13b
20	13.95 $\pm$ 0.69c	9.00 $\pm$ 0.43c
100	26.48 $\pm$ 1.26d	17.54 $\pm$ 0.94d
200	40.31 $\pm$ 2.80e	22.46 $\pm$ 1.69e
300	43.70 $\pm$ 2.51e	22.93 $\pm$ 1.40e

<sup>a</sup> Means within a column followed by the same letter are not significantly different ( $P < 0.05$ ; Fisher's protected LSD test)

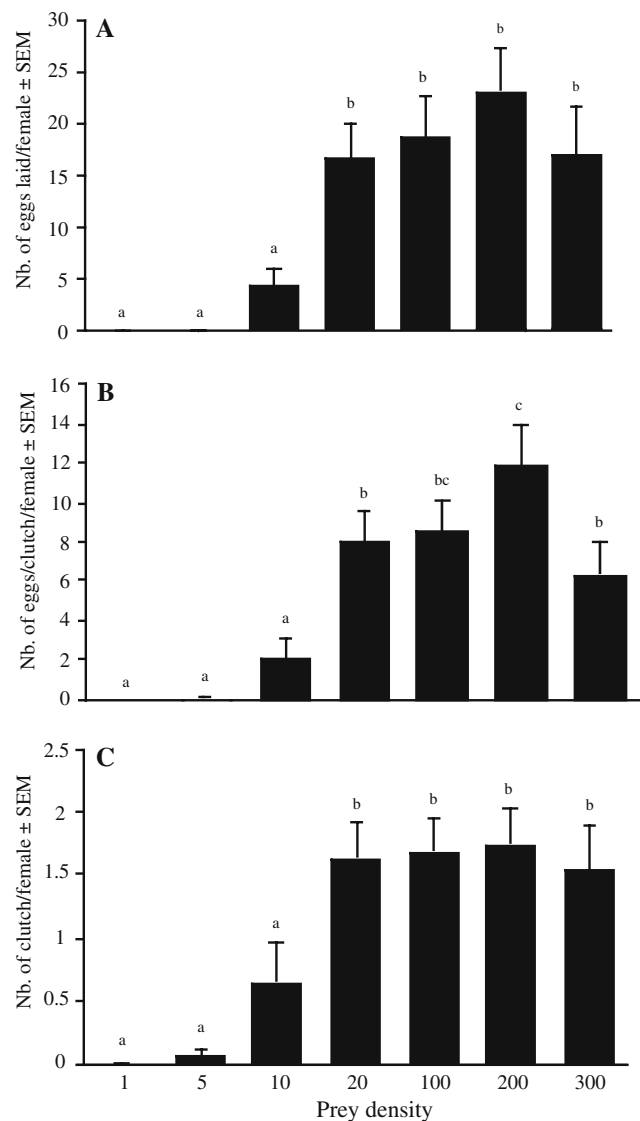


**Fig. 1** Mean change in body weight (milligrams  $\pm$  SE) of *Coccinella undecimpunctata* females when placed on seven different prey densities for 3 days. Histograms with the same letter are not significantly different ( $P < 0.05$ ; Fisher's Protected LSD test)

Fig. 3B). Female body weight was not significantly affected by either the species or sex of the beetles they were kept with (Table 2).

Fecundity of *C. undecimpunctata* females was not significantly reduced in the presence of conspecifics (ANOVA,  $F = 0.009$ ,  $df = 37$ ,  $P = 0.927$ ; Fig. 3C) but was in the presence of heterospecifics (ANOVA,  $F = 6.88$ ,  $df = 38$ ,  $P \leq 0.0001$ ; Fig. 3D). *C. undecimpunctata* fecundity was not affected either by the gender of the conspecifics (ANOVA,  $F = 0.548$ ,  $df = 36$ ,  $P = 0.583$ ; Fig. 3C) or heterospecifics (ANOVA,  $F = 3.356$ ,  $df = 37$ ,  $P = 0.046$ ; Fig. 3D). The mean number of eggs laid by *C. undecimpunctata* was significantly affected by the presence of another lady beetle species independent of its sex (Table 2).

The presence of conspecifics did not significantly affect the clutch size of *C. undecimpunctata* (ANOVA,  $F = 0.249$ ,  $df = 37$ ,  $P = 0.621$ ; Fig. 3E), but clutch size was significantly lower in the presence of heterospecifics (ANOVA,  $F = 7.45$ ,  $df = 38$ ,  $P = 0.01$ ; Fig. 3F).

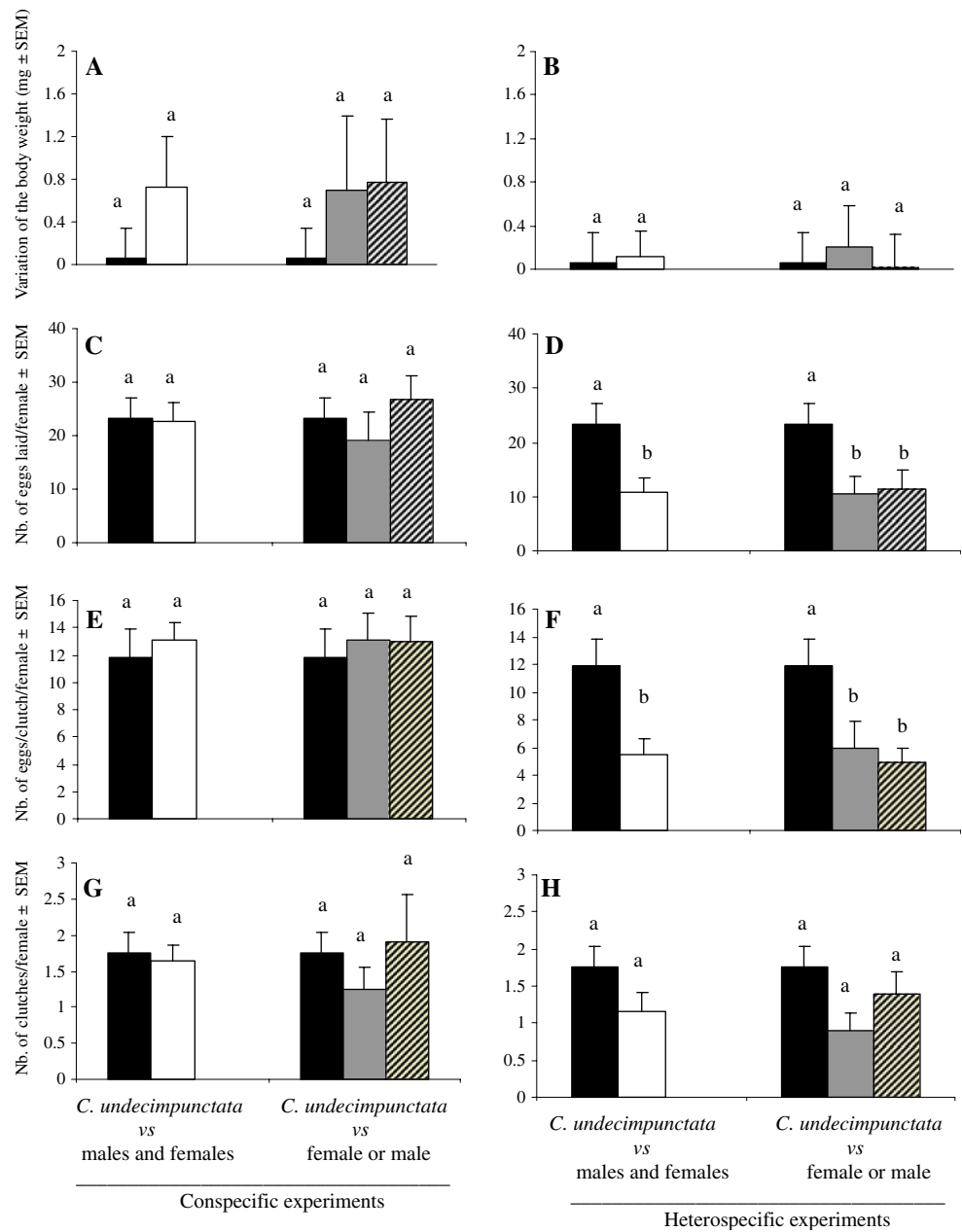


**Fig. 2** Reproductive capacity [A fecundity (mean number of eggs per day per female  $\pm$  SE), B clutch size (mean number of eggs per day per clutch  $\pm$  SE) and C clutch number (mean number of clutches per day per female  $\pm$  SE)] of *Coccinella undecimpunctata* females in 24 h on seven different prey densities. Histograms with the same letter are not significantly different ( $P < 0.05$ ; Fisher's Protected LSD test)

Mean clutch size was not significantly affected either by the sex of the conspecifics (ANOVA,  $F = 0.123$ ,  $df = 36$ ,  $P = 0.885$ ; Fig. 3E) or heterospecifics (ANOVA,  $F = 3.68$ ,  $df = 37$ ,  $P = 0.035$ ; Fig. 3F). The mean number of eggs per clutch laid by *C. undecimpunctata* was significantly affected by the presence of another lady beetle species independent of sex (Table 2).

The presence of a conspecific or heterospecific did not significantly affect the mean number of clutches laid by *C. undecimpunctata* (ANOVA,  $F = 0.063$ ,  $df = 37$ ,  $P = 0.803$ ; Fig. 3G; ANOVA,  $F = 2.27$ ,

**Fig. 3** Mean changes in body weight (**A, B**), mean number of eggs laid (**C, D**), mean number of eggs per clutch per female (**E, F**) and mean number of clutches per female (**G, H**) of *Coccinella undecimpunctata* females in the presence of ladybird beetles (*C. undecimpunctata* or *Harmonia axyridis*). Histograms within the same subgroup of experiments having the same letter are not significantly different ( $P < 0.05$ ; Fisher's protected LSD test). *Closed bars* *C. undecimpunctata* females kept alone; *open bar* *C. undecimpunctata* females in the presence of conspecifics or heterospecifics; *gray bar* *C. undecimpunctata* females in the presence of a female conspecific or heterospecific; and *dashed bar* *C. undecimpunctata* in the presence of a male conspecific or heterospecific



df = 38,  $P = 0.140$ ; Fig. 3H). Similarly, the mean number of clutches was not affected by the gender of the conspecific (ANOVA,  $F = 1.446$ , df = 36,  $P = 0.249$ ; Fig. 3G) or heterospecific (ANOVA,  $F = 1.52$ , df = 38,  $P = 0.399$ ; Fig. 3H). Mean number of clutches laid by *C. undecimpunctata* was independent of the presence or sex of another lady beetle (Table 2).

**Discussion**

Voracity and reproductive capacity of coccinellids depends on prey density. The increase in prey density

results in the increase of the number of prey eaten and its reproductive numerical response (Hodek and Honěk 1996). The results of this study showed that when provided with 200 aphids per day, females of *C. undecimpunctata* were most voracious, achieved their reproductive potential and maintained body weight. However, reproductive capacity of *C. undecimpunctata* females increases and then levelled off at numbers of aphids provided greater than 20. This may have occurred because coccinellids have a genetically fixed fecundity that is manifest when food is plentiful and environmental conditions are favorable (Hodek and Honěk 1996). Over the range of 20–200 aphids

**Table 2** Two-factor ANOVA for body weight increase and reproductive performance of *Coccinella undecimpunctata* females in the presence of females or males of conspecifics or heterospecifics ( $P < 0.05$ )

Dependent variable source	df	F	P
Body weight increase			
Between lady beetles species	1, 39	1.354	0.252
Between sex	1, 39	0.011	0.917
Interaction species $\times$ sex	1, 39	0.072	0.790
Mean number of eggs laid			
Between lady beetles species	1, 39	7.459	0.010
Between sex	1, 39	0.955	0.335
Interaction species $\times$ sex	1, 39	0.634	0.431
Mean number of eggs per clutch			
Between lady beetles species	1, 39	16.940	$\leq 0.0001$
Between sex	1, 39	0.100	0.754
Interaction species $\times$ sex	1, 39	0.050	0.825
Mean number of clutches			
Between lady beetle species	1, 39	1.467	0.234
Between sex	1, 39	2.685	0.110
Interaction species $\times$ sex	1, 39	0.046	0.832

provided per day the mean number of eggs per clutch increased significantly. These results suggest that *C. undecimpunctata* females maximize their fitness by laying large clutches.

In sharing a local prey population, predators may disturb each other's foraging success (Evans 1991, 2004) and reproductive capacity (Agarwala et al. 2003; Kajita et al. 2006) and put eggs at risk of interspecific predation (Agarwala and Yasuda 2001). Even when the resource is not in short supply, our results suggested that *H. axyridis* had a negative impact on *C. undecimpunctata* fitness, since fecundity was significantly affected in the presence of a heterospecific and predation of eggs occurred (an average of  $21.6 \pm 8.6\%$  of the eggs laid were eaten by *H. axyridis* adults). Exploitative competition was not the cause of the lower fecundity of *C. undecimpunctata*. Indeed, only  $68.5 \pm 6.2\%$  of the aphids provided were consumed. Interference competition due to the presence of a heterospecific could explain the results. So far, the mechanism for this lower fecundity is not clear. However, one of the possible explanations is that *C. undecimpunctata* expended some time and/or matter and/or energy on competition or avoiding competition, and then there was less of these resources available for reproduction. Although *H. axyridis* females ate more aphids than did males, they did not differ in their effect on the growth and reproductive capacity of *C. undecimpunctata*. These facts suggest that, independent of the gender of the heterospecific, interference competition could affect the population abundance of a coccinellid by reducing its reproductive capacity. Contrary to our prediction, the presence of a conspe-

cific did not affect the reproductive performance of *C. undecimpunctata* females. The decreasing of fecundity through interference competition may be due to the absence of co-occurrence of *H. axyridis* and *C. undecimpunctata* in the Azorean ecosystem. Indeed, *H. axyridis* has not yet been introduced into the Azores.

The most surprising result was that the body weight of female *C. undecimpunctata* was unaffected by the presence of *H. axyridis*. This suggests that in the presence of *H. axyridis*, resources were first used for basal metabolism and body weight maintenance. This could be advantageous for females, enabling them to use their reserves to locate new patches of prey in which the conditions are more suitable for their offspring. Recent results demonstrate that the invasive ladybird beetle *C. septempunctata* influences the distribution and abundance of a native competitor, not only by reducing its survivorship in alfalfa fields in Utah, USA, but also by altering its dispersal and habitat use across the landscape (Evans 2004). These results suggest that one of the possible mechanisms involved in change in habitat use by coccinellids after the arrival of exotic heterospecifics could be related to the way that energy is used in reproduction and maintenance.

The arrival of *H. axyridis* in natural and agricultural ecosystems is associated with significant reductions in population size of several coccinellid species (Colunga-Garcia and Gage 1998). The introduction of *C. septempunctata* into the USA resulted in a population decrease in the smaller species *Adalia bipunctata* L. and *C. transversoguttata richardsoni* Brown (Elliot et al. 1996). The subsequent invasion by *H. axyridis* resulted in the displacement of *C. septempunctata* from its dominant position (Elliot et al. 1996; Brown and Miller 1998; Turnock et al. 2003) and the competitive displacement of *C. sanguinea* from citrus ecosystems in Florida, USA (Michaud 2002). Interference competition may cause ladybirds to fall off a plant, to switch from intensive to extensive search or to cease feeding (Ferran and Dixon 1993). It may also result in a decrease in fitness due to IGP (Yasuda and Shinya 1997; Michaud 2002; Félix and Soares 2004) and competition for prey (Evans 1991). It is difficult to speculate on the potential long-term impact of *H. axyridis* in the field (Lucas et al. 2002) because the other native species may respond differently. For example, *A. bipunctata* in Siberia avoids some species of plants, mainly *Salix* sp., where *H. axyridis* is present (Iablokoff-Khnzorian 1982). Nevertheless, based on the results obtained by Félix and Soares (2004) on the negative impact *H. axyridis* has on other coccinellid species and the

results presented here, the introduction of *H. axyridis* could endanger the population abundance and/or induce competitive displacement of *C. undecimpunctata* from the Azorean ecosystem.

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