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

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INTRODUCTION

A number of studies have revealed that invading species, including the ladybird beetle predator *Harmonia axyridis* Pallas, have a negative impact on native species assemblages. Invading species may have important effects on the dynamics and composition of guilds of established species, as the invaders can interact with established species, directly or indirectly, including through intraguild predation (Elliott et al., 1996; LaMana and Miller, 1996; Yasuda and Shinya, 1997; Brown and Miller, 1998; Colunga-Garcia and Gage, 1998; Obrycki et al., 1998; Lucas et al., 2002; Yasuda et al., 2001; Michaud, 2002; Turnock et al., 2003; Evans, 2004). However, how the introduced species displace native species is often poorly understood (Evans, 2004).

Competition may occur indirectly when two or more ladybeetles use the same resources and when those resources are in short supply (exploitative competition). Competition may also occur through more direct interactions. It occurs when the organisms seeking a resource harm one other in the process, even if the resource is not in short supply (interference competition). Interaction between the two organisms reduces the fitness and/or equilibrium population density of each. This can occur in several ways. By requiring that an organism expend some of its time and/or matter and/or energy on competition or the avoidance of competition, a competitor may effectively reduce the amounts left for maintenance and reproduction (Krebs, 1994).

The aims of this study were to determine (i) the functional and the reproductive numerical responses of *Coccinella undecimpunctata* L. females (native aphidophagous predator of the Azores) on diets of *Aphis fabae* Scopoli; (ii) the effect of the presence of the adults of conspecifics or the heterospecific *H. axyridis* on growth and reproductive capacity of *C. undecimpunctata* females; and (iii) to foresee the potential impact of the introduction of the exotic *H. axyridis* on the fitness of the native *C. undecimpunctata*.

MATERIAL AND METHODS

Biological features of *C. undecimpunctata* females fed on different prey density of *A. fabae*. The number of apterous females of *A. fabae* eaten in 24h by fifteen day old females of *C. undecimpunctata* was determined. Seven treatments corresponding to seven prey densities were conducted, in which 1, 5, 10, 20, 100, 200 and 300 individuals of *A. fabae* were provided to ovipositing females. Females were fifteen day old after sexual maturation, approximately half of their longevity. Twenty replicates were conducted per treatment. All experiments were done at 25±1 °C, 75±5 % RH and a photoperiod of L16: D8 under fluorescent lamps. The females' voracity and reproductive capacity were recorded over the final 24h of the three day experimental period. The females' body weight increase was estimated over the 72h experimental period.

Functional response of *C. undecimpunctata* females fed on *A. fabae*. Data on females voracity were fit to the "random-predator" equation (Rogers, 1972), a modification of Holling's (1959) disk equation.

Impact of the presence of conspecific and hetrospecific adults on the growth and reproductive capacity of *C. undecimpunctata* females. Two treatements with 20 replicates each were conduced, in which one adult of *C. undecimpunctata* or one adult of *H. axyridis* with, approximately, half of their longevity was added to experimental cages with a single *C. undecimpunctata* female. Caged females of *C. undecimpunctata* were fed, over a three day period, with a daily amount of 200 apterous *A. fabae*. *C. undecimpunctata* or *H. axyridis* were added to the experimental set up at the start of the third day. The adults added to experimental set up were reared under the same diet of caged females. Ten females and ten males were used in each treatment. Abiotic conditions and age of the *C. undecimpunctata* females maintained in the experimental set up were as previously described. For the third day, body-weight and reproductive capacity of *C. undecimpuncata* females was recorder. In the replicates were 2 females of *C. undecimpunctata* were maintained for 24 h, the biological parameters of reproductive capacity was compared and presented per single individual.

RESULTS

Biological features of *C. undecimpunctata* females fed on different prey densities of *A. fabae*. The number of aphids eaten (ANOVA, $F= 129.96$, $d.f.= 6, 139$, $P<0.0001$) and the amount of biomass ingested (ANOVA, $F=108.14$, $d.f.=6$, $P<0.0001$) by *C. undecimpunctata* females in 24h increased with prey density and reached the maximum value when 200 prey were provided (Fig. 1).

Changes in the body weight of *C. undecimpunctata* females over the 72h experimental period, differed significantly between prey densities (ANOVA, *F*=24.63, *d.f.*=6, 139, *P*<0.0001) (Fig. 2). Female body weight decreased significantly over the three-day period at prey densities below 100 aphids. At prey densities of 200 and 300 aphids an increase in body weight was observed (Fig. 2).
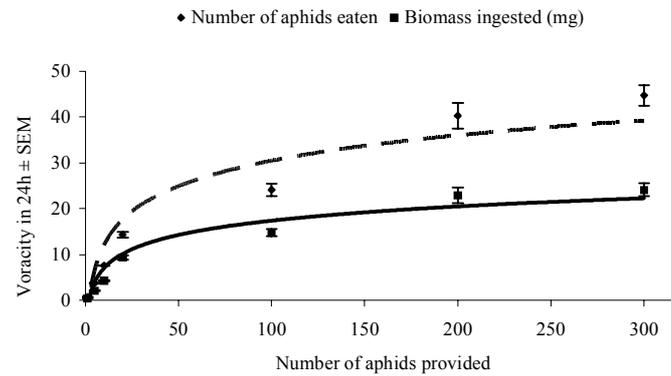
Figure 1. Functional response of *C. undecimpunctata* females in 24h, fed on seven prey densities, expressed as the number of aphids consumed (R^2=0.84) and mg of biomass ingested (R^2=0.84). Models of "random-predator" equation (Rogers, 1972) were calculated and plotted for untransformed data, using the non-linear regression module of SPSS v. 11.5
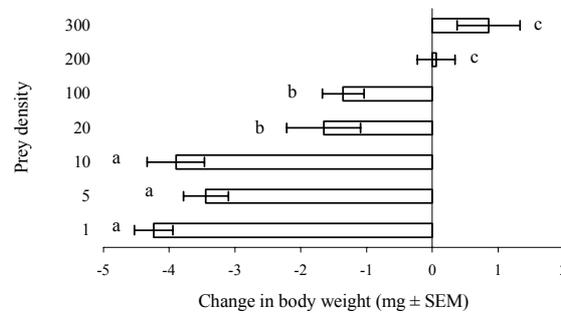
Figure 2. Mean change in body weight (mg ± SE) of *C. undecimpunctata* females when placed on seven prey densities for three days. Histograms with the same letter are not significantly different (P < 0.05; Fisher's Protected LSD test).

Fecundity differed significantly with prey density (ANOVA, *F*=9.97, *d.f.*=6, *P*< 0.0001) (Fig. 3A). The number o eggs significantly increased up to a prey density of 20 aphids, and levelled of at higher prey densities (Fig. 3A).

Mean clutch size, differed significantly with prey density (ANOVA, *F*=12.1, *d.f.*=6, *P*<0.0001) (Fig. 3B). Clutch size significantly increased up to prey density of 200 aphids (Fig. 2B), at which clutch size was maximal. A reduction in clutch size was noted at prey density of 300 aphids (Fig. 3B).

The clutch number, differed significantly with prey density (ANOVA, *F*=9.82, *d.f.*=6, *P*<0.0001) (Fig. 3C). Clutch number significantly increased up to a prey density of 20 aphids, and levelled of at higher prey densities (Fig. 3C).
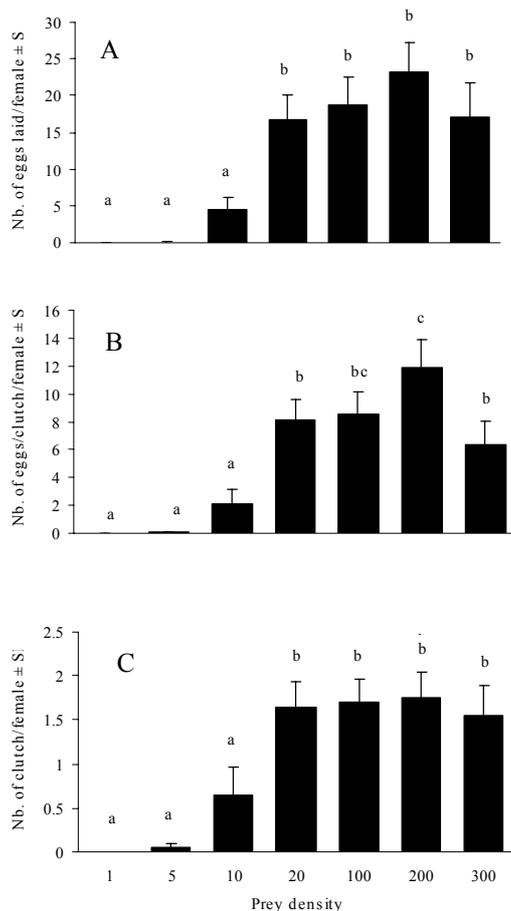
Figure 3. Reproductive capacity [A: Fecundity (mean number of eggs per day per female ± SE), B: clutch size (mean number of eggs per day per clutch per female± SE) and C: clutch number (mean number of clutches per day per female ± SE)] of *C. undecimpunctata* females in 24h, on seven prey densities. Histograms with the same letter are not significantly different (P < 0.05; Fisher's Protected LSD test).

Functional response of *C. undecimpunctata* females fed on *A. fabae*. The data fit to the modified Holling disk equation showed that the number of prey consumed and the amount of ingested biomass in 24 h increased (but at a decreasing rate) with increasing prey density, which typical of a type II functional response (Fig. 1). Estimated models accounted for a significant portion of the initial variance of the data, both for voracity (F=892.12, $d.f.$=6, P<0.05, R^2=0.84) and for relative consumption rate (F=776.29, $d.f.$=6, P<0.05, R^2=0.83). The estimated parameter values were a=0.6124 and Th=0.1751 for voracity, and a=0.4873 and Th=0.0356 for relative consumption rate (Fig. 1).

Impact of the presence of conspecific and hetrospecific adults on the growth and reproductive capacity of *C. undecimpunctata* females. No significant differences were found in changes in body weight of *C. undecimpunctata* females in the absence and in the presence of the conspecific (ANOVA, F=1.514, $d.f.$=37, P=0.226; Fig. 4A) and the hetospecific (ANOVA, F=0.066, $d.f.$=38, P=0.799; Fig. 4B). Changes in body weight of *C. undecimpunctata* females did not differ according to *C. undecimpunctata* (ANOVA, F=0.743, $d.f.$=36, P=0.483; Fig. 4A) and *H. axyridis* genders (ANOVA, F=0.29, $d.f.$=37, P=0.749; Fig. 4B). Female's body weight was not significantly affected by ladybeetle species and sex (Table 1).

Fecundity of *C. undecimpunctata* females was not significantly decreased in the presence of the conspecific (ANOVA, F=0.009, $d.f.$=37, P=0.927; Fig. 4C), however, in the presence of the heterospecifc, fecundity of *C. undecimpunctata* females was significantly decreased (ANOVA, F=6.88, $d.f.$=38, P<0.0001; Fig. 4D). *C. undecimpunctata* fecundity was not affected, either by conspecific (ANOVA, F=0.548, $d.f.$=36, P=0.583; 4C) and heterospecific gender (ANOVA, F=3.356, $d.f.$=37, P=0.046; Fig. 4D). Mean number of eggs laid by *C. undecimpunctata* was significantly affected by ladybeetle species and but not by the sex (Table 1).

No significant differences were found in *C. undecimpunctata* clutch size in the absence and the presence of conspecific (ANOVA, F=0.249, $d.f.$=37, P=0.621; Fig. 4E), however, clutch size was significantly lower in the presence of the heterospecific (ANOVA, F=7.45, $d.f.$=38, P=0.01; Fig. 4F). Mean clutch size was not significantly affected, either by conspecific (ANOVA, F=0.123, $d.f.$=36, P=0.885; 4E) and heterospecific gender (ANOVA, F=3.68, $d.f.$=37, P=0.035; Fig. 4F). Mean number of eggs per clutch laid by *C. undecimpunctata* was significantly affected by ladybeetle species and but not by the sex (Table 1).
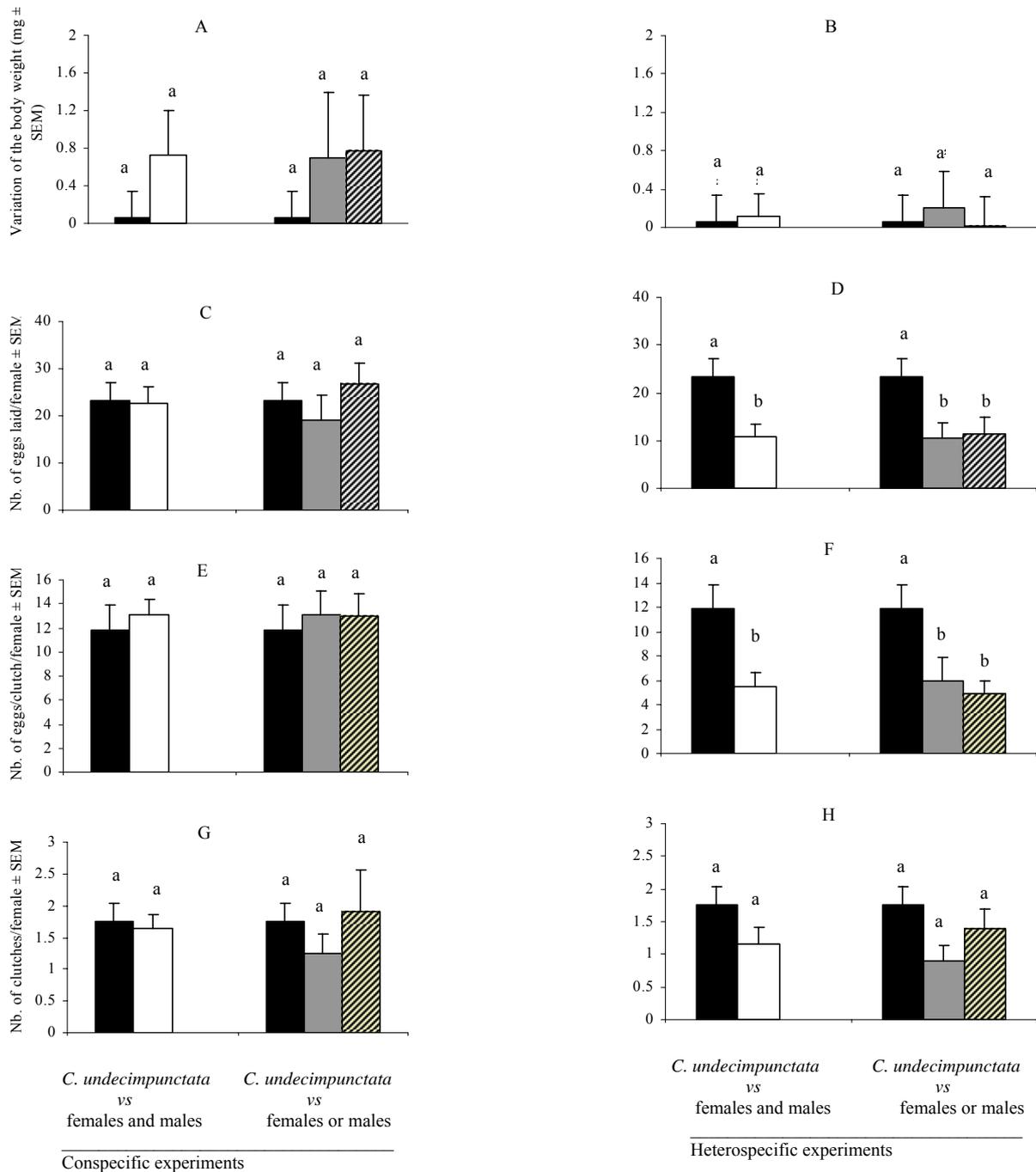
Figure 4. Mean changes in body-weight (A and B), mean number of eggs laid (C and D), mean number of eggs per clutch per female (E and F) and mean number of clutches per female (G and H) of *C. undecimpunctata* females, in the presence of ladybird beetles (*C. undecimpunctata* and *H. axyridis* respectively). 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 conspecific or heterospecific; gray bar *C. undecimpunctata* females in the presence of a female of conspecific or heterospecific and dashed bar *C. undecimpunctata* in the presence of a male conspecific or heterospecific.

No significant differences were observed in the mean number of clutches laid by *C. undecimpunctata* females in the presence or absence of the conspecific (ANOVA, *F*=0.063, *d.f.*=37, *P*=0.803; Fig. 4F) and also in the presence or absence of the heterospecific (ANOVA, *F*=2.27, *d.f.*=38, *P*=0.140; Fig. 4G). The mean number of clutches was not affected by gender, either in the presence of conspecific (ANOVA, *F*=1.446, *d.f.*=36, *P*=0.249; Fig. 4F) and in the presence of the heterospecific (ANOVA, *F*=1.52, *d.f.*=38, *P*=0.399; Fig. 4G). Mean number of clutches laid by *C. undecimpunctata* was not significantly affected by ladybeetle species and sex (Table 1).

Table 3. Two-factor ANOVA for body weight increase and reproductive performance of *C. undecimpunctata* females in the presence of females or males of conspecifics or heterospecific (P < 0.05).

Source	d.f.	F	P
Body weight increase			
Between ladybeetles species	1, 39	1.354	0.252
Between sex	1, 39	0.011	0.917
Interaction species x sex	1, 39	0.072	0.790
Mean number of eggs laid			
Between ladybeetles species	1, 39	7.459	0.010
Between sex	1, 39	0.955	0.335
Interaction species x sex	1, 39	0.634	0.431
Mean number of eggs per clutch			
Between ladybeetles species	1, 39	16.940	≤0.0001
Between sex	1, 39	0.100	0.754
Interaction species x sex	1, 39	0.050	0.825
Mean number of clutches			
Between ladybeetles species	1, 39	1.467	0.234
Between sex	1, 39	2.685	0.110
Interaction species x sex	1, 39	0.046	0.832

DISCUSSION

Overlapping oviposition places eggs at potential risk of interspecific predation in unstable aphid colonies (Agarwala and Yasuda 2001). Furthermore, by sharing a local prey population, predators may disturb each other's foraging success (Evans 1991, Evans, 2004) and reproductive capacity (Agarwala et al., 2003). Even when the resource is not in short supply, that is at high prey density, we demonstrated that the presence of *H. axyridis* had a negative impact on *C. undecimpunctata* fitness, since fecundity was significantly affected in the presence of the heterospecific and because interspecific predation on eggs occurred (an average of 21.6±8.6% of the eggs laid were eaten by *H. axyridis* adults). It is noteworthy that, under low prey density, no significant difference on *C. undecimpunctata* reproductive capacity, at the presence and absence of the heterospecific, was observed (unpublished data). This fact suggest that, although the strong pressures imposed by short food supply and the presence of one heterospecific, the females of *C. undecimpunctata* were able to maintained a minimal capacity of reproduction and protecting, by this way, the survival of is own species. Exploitative competition was not the cause for lower fecundity. Indeed we found that only 68.5±6.2% of the aphids provided were consumed by both species. Interference competition due to the presence of a heterospecific could explain the results obtained. We found that although *H. axyridis* females ate more *A. fabae* than males, no significant differences occurred between the presence of a heterospecific female or male for *C. undecimpunctata* growth and reproductive capacity. These facts suggest that, independently of heterospecific gender, interference competition has the potential to play an important role in reduction of coccinellid abundance through the decrease of reproductive capacity of the coccinellids.

The most surprising result was that, while decreasing reproductive performance, *C. undecimpunctata* females' body weight was unaffected by the presence of *H. axyridis*. This result suggests that, in the presence of *H. axyridis*, resources were preferentially used for basal metabolism instead of reproduction. This situation could be advantageous to females, enabling them to use energy in

extensive search and thus to locate new patches in which the conditions should be more advantageous to offspring. Most recent results were able to demonstrate that the introduced *Coccinella septempunctata* L. influence the distribution and abundance of native competitor, not only by reducing the survivorship in alfalfa fields, but also by altering the dynamic of dispersal and habitat use across the landscape (Evans, 2004).

Nevertheless, based on the results obtained by Félix and Soares (2004), the examples of negative impacts that *H. axyridis* may have on other coccinelid species, and the results presented in our experiments here, we suggest that the introduction of *H. axyridis* could endanger the population abundance and /or induce competitive displacement of *C. undecimpunctata* in the Azorean ecosystem.

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