Entomologia
Experimentalis et Applicata

DOI: 10.1111/j.1570-7458.2011.01202.x

Biotic interactions between *Eriopis connexa* and *Hippodamia variegata*, a native and an exotic coccinellid species associated with alfalfa fields in Chile

A. A. Grez[1]*, B. Viera[1] & A. O. Soares[2,3]

[1]*Facultad de Ciencias Veterinarias y Pecuarias, Universidad de Chile, Casilla 2, Correo 15, La Granja, Santiago, Chile,* [2]*CIRN, Department of Biology, University of the Azores, 9500-801 Ponta Delgada, Azores, Portugal, and* [3]*Azorean Biodiversity Group – CITA-A, University of the Azores, Departamento de Ciências Agrárias, Terra-Chã, 9701-851 Angra do Heroísmo, Azores, Portugal*

Accepted: 14 October 2011

Key words: cannibalism, intraguild predation, intraspecific and interspecific competition, laboratory experiments, predator–predator interactions, Coleoptera, Coccinellidae, *Medicago sativa*, Fabaceae, *Acyrthosiphon pisum*, Hemiptera, Aphididae

Abstract

Human-assisted introductions, including those in the context of biological control, are considered to be one of the most important factors of global environmental change. However, the mechanisms underlying environmental changes, such as a decrease in the relative abundance of native species, are poorly understood. Since the introduction of the ladybird beetle, *Hippodamia variegata* (Goeze) (Coleoptera: Coccinellidae), in Chile in the 1970s for biological control of aphids, a reduction in the relative abundance of the native ladybird beetle *Eriopis connexa* (Germar) has been noticed. To explore the role of cannibalism, intraguild predation (IGP) or competition as possible mechanisms that might increase dominance of *H. variegata* over *E. connexa*, several laboratory experiments were carried out. The native and the exotic species were very similar in their voracity and biotic interactions. Although *H. variegata* was able to maintain constant reproductive performance, *E. connexa* reproduction decreased at lower densities of aphids, *Acyrthosiphon pisum* (Harris) (Hemiptera: Aphididae). The impacts of cannibalism, IGP, and competition exerted by these species were very symmetrical in both larvae and adults. We conclude that these biotic factors may not fully explain the increase in relative abundance of *H. variegata*. The higher sensitivity of *E. connexa* to prey patch size, along with other factors such as chemical-mediated negative interspecific interactions may be operating in alfalfa fields, changing the composition of associated coccinellid assemblages.

Introduction

Human-assisted introductions are considered to be one of the most important mechanisms of global environmental change and the second leading threat to worldwide biodiversity after habitat destruction (Vitousek et al., 1996, 1997; Pimentel et al., 2000). Generalism and ecological flexibility make species more likely to become established and integrated into new regions (Simberloff, 1996; Simberloff & Stiling, 1996; Williamson, 1996; Shigesada & Kawasaki, 1997). However, information on how interspecific interference mechanisms may mediate successful introductions is often lacking.

Releases of the ladybird beetles, *Coccinella septempunctata* (L.), *Harmonia axyridis* (Pallas), and *Propylea quatordecimpunctata* (L.), in North America have led to displacements, reductions in abundance and changes in habitat use of the native species (Elliot et al., 1996; Brown & Miller, 1998; Evans, 2000; Turnock et al., 2003; Alyokhin & Sewell, 2004; Mills, 2006; Evans et al., 2011). Evidence appears to support the idea that intraguild predation (IGP) (LaMana & Miller, 1996; Brown & Miller, 1998;

*Correspondence: A. A. Grez, Facultad de Ciencias Veterinarias y Pecuarias, Universidad de Chile, Casilla 2, Correo 15, La Granja, Santiago, Chile. E-mail: agrez@uchile.cl

Kajita et al., 2000; Michaud, 2002; Félix & Soares, 2004; Snyder et al., 2004; Yasuda et al., 2004; Nóia et al., 2008; Ware et al., 2009) and exploitative competition (Mills, 2006) may be some of the mechanisms limiting the coexistence of species. However, the role of other key mechanisms, such as cannibalism and interspecific competition (either exploitative, interference, or apparent competition), has been less studied.

Theory predicts that the usual outcome of exploitative and interference competition is the competitive exclusion of the weaker competitor. Theory also predicts that permanent coexistence of competing populations is only possible if the negative effect of each species on the members of its own population (cannibalism) is greater than its effect on the competitor (Koch, 1974; Berryman & Kindlmann, 2008; Crowder & Snyder, 2010). However, in agro-ecosystems, it is very common to find assemblages of several competing natural enemies on shared hosts. Temporal and spatial partitioning of the resources and self-limitation may be important mechanisms explaining this competitive coexistence (Mills, 2006). For instance, a field cage study conducted on sweet corn in Minnesota (USA) showed that *H. axyridis* larvae weighed more when kept with *Coleomegilla maculata* De Geer than when kept with an equal number of conspecifics, suggesting that intraspecific competition is stronger for *H. axyridis* than interspecific competition with *C. maculata* (Hoogendoorn & Heimpel, 2004). The coexistence of *Adalia bipunctata* (L.) and *C. maculata*, also in corn fields in Minnesota, was attributed to a spatial partitioning of oviposition behaviour; the two species preferred the top and the bottom part of the plants, respectively. In this case, the role of egg cannibalism was stronger than interspecific predation of eggs (Schellhorn & Andow, 1999).

In central Chile, as many as 14 native and exotic species of coccinellids have been found in alfalfa, *Medicago sativa* L. (Fabaceae) fields (Zaviezo et al., 2004, 2006; Grez et al., 2008, 2010). Among the most abundant species are *Hippodamia variegata* (Goeze) and *Eriopis connexa* (Germar) (both Coleoptera: Coccinellidae). The former was imported as a biological control agent from South Africa in the 1970s, whereas the latter is endemic to southern South America and is widely distributed in Chile (Hoffman, 1970; Montes, 1970). Both species coexist in alfalfa fields throughout the growing season, even at small spatial scales (Zaviezo et al., 2006), but there is temporal segregation of their peak abundances. *Eriopis connexa* reaches its highest abundance in spring or early summer when aphid populations are also abundant, and strongly declines in summer, when aphids become scarce. In contrast, *H. variegata* increases its abundance in summer and also in autumn (Grez, 1997; Grez et al., 2004, 2005). We have followed the dynamics of these species in central Chile for 20 years, and have noticed an increase in the numerical dominance of *H. variegata* over *E. connexa* populations in the last few years (Figure 1). Seasonal and long-term population dynamics suggest that the exotic *H. variegata* may have a competitive advantage over *E. connexa* in central Chile, as has occurred with other coccinellid assemblages around the world (e.g., Obrycki et al., 1998; Turnock et al., 2003; Evans, 2004).

The main goal of the present study was to explore, under laboratory conditions, the roles of cannibalism, IGP, and interference competition as possible mechanisms to explain the relative abundances of *E. connexa* and *H. variegata* in alfalfa fields in Chile. We determined (1) the voracity and fitness of *E. connexa* and *H. variegata* provided with different numbers of *Acyrthosiphon pisum* (Harris) (Hemiptera: Aphididae); (2) the occurrence of IGP and cannibalism among fourth instars of both species and among larvae and eggs in the presence and absence of aphids; and (3) the role of intraspecific and interspecific competition among larvae or adults on voracity, growth, and reproductive capacity.

As *H. variegata* is increasing its relative abundance over *E. connexa* in the field, one of the following four scenarios may be operating: (1) *H. variegata* should have higher fitness exploiting food resources; (2) *H. variegata* should have a superior ability to exert IGP on *E. connexa*; (3) cannibalism within *H. variegata* could be lower than within *E. connexa*; or (4) the impact of intraspecific competition

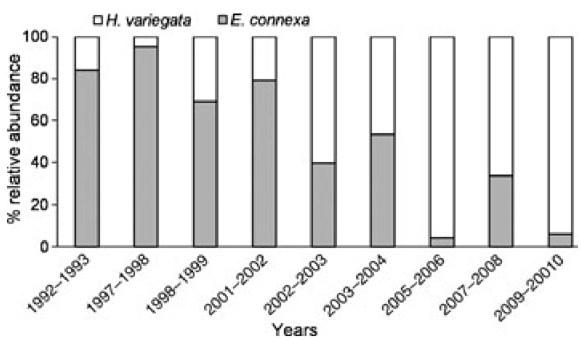

Figure 1 Relative abundance of *Hippodamia variegata* and *Eriopis connexa* in crops in central Chile from 1991 to 2010. In some years, data are missing due to lack of sampling. Data are unpublished and from Grez (1997) and Grez et al. (2004, 2008, 2010), and correspond to samples taken from the same place and at the same time of the year, with the same sampling protocol and effort.

may be lower than interspecific competition with *E. connexa*. These scenarios could operate simultaneously.

Materials and methods

Fitness of *Eriopis connexa* and *Hippodamia variegata* females provided with different numbers of *Acyrthosiphon pisum*

Our experiments were carried out in the laboratory following the methodology used by Félix & Soares (2004) and Soares & Serpa (2007). We placed two alfalfa shoots (15 cm long) in a small transparent plastic vial filled with moistened sand. After infesting the shoots with 5, 10, 20, 30, 40, 80, 100, or 120 fourth and fifth instars of *A. pisum*, we added one *E. connexa* or *H. variegata* adult female, collected in alfalfa fields and starved for 24 h before the experiments. We used these aphid densities based on Soares & Serpa (2007), who found that the reproductive parameters for *Coccinella undecimpunctata* (L.) (a coccinellid species similar in size to those used in our experiments) varied significantly between 5 and 20 aphids and were similar at higher densities. Each vial was enclosed with a transparent plastic cone (10 cm diameter × 22 cm high), covered with a fine mesh on the top, not touching the alfalfa shoots. They were left in a growth chamber (at 25 °C, 50% r.h., and L16:D8) for 3 days, and aphids were replaced daily. The number of replicates for each aphid density was 13 for *E. connexa* and 12 for *H. variegata*.

The voracity of coccinellids was recorded over the final 24 h of the 3-day experimental period, whereas the change in female body weight was estimated over the whole 3-day period. Voracity (V_o) was calculated as (Soares et al., 2003):

$$V_o = A - a_{24} \times ra_{24},$$

where V_o is the number of aphids eaten, A is the number of aphids provided, a_{24} is the number of aphids alive after 24 h, and ra_{24} is the survival of aphids after 24 h in the absence of the predator. Body weight of the coccinellids was measured at the beginning and at the end of each experiment using a 10^{-4} mg Denver AA200 analytical balance (Denver Instrument, Bohemia, NY, USA).

To analyse the effect of aphid density on the reproductive capacity of *E. connexa* and *H. variegata*, we performed experiments similar to those described above, but used females reared in the laboratory. Aphid densities were 5, 20, and 80, with 15 replicates per coccinellid species. Females were 15 days old, which is when they have maximum fecundity, similar to other ladybird species (Lanzoni et al., 2004). The reproductive capacity of each coccinellid species was measured as the number of eggs and clutches laid per female per day. A one-way ANOVA followed by a multiple comparison test [Fisher's protected least significant difference (LSD) test] was used to compare voracity, body-weight variation and reproductive capacity, and a t-test was used to compare voracity of *E. connexa* and *H. variegata* at each prey density (SPSS, 2006).

Intraguild predation and cannibalism

Using two alfalfa shoots (15 cm tall) enclosed inside a transparent plastic cone similar to those used before, we set up different conspecific and allospecific combinations of eggs and fourth instars (Table 1). Also, a single *E. connexa* or *H. variegata* larva was used as a control treatment. All of these combinations were tested under two aphid densities (0 or 60 aphids), simulating scenarios that naturally occur in alfalfa fields in central Chile, in summer when aphids are scarce, but coccinellids are still present, or in spring and autumn, when aphids are abundant (Apablaza & Stevenson, 1995; Grez et al., 2005). There were 15 replicates of each treatment. We used fourth instars (starved for 24 h) because they are more voracious and aggressive than younger instars (Nóia et al., 2008). In the combinations with eggs, five eggs were provided (Félix & Soares, 2004). Vials were kept in a growth chamber under the same abiotic conditions as the previous experiments; after 24 h, the shoots were checked to determine the mortality of eggs and larvae. Intraguild predation levels were estimated from the rates of predation (the proportion of replicates in which IGP occurred).

Logistic analyses corrected for overdispersion were used to compare the rates of IGP and cannibalism between *E. connexa* and *H. variegata* under the experimental conditions described before. Statistical analyses were performed with the GenStat statistical package, version 12 (VSN International, Hemel Hempstead, UK).

Competition between *Eriopis connexa* and *Hippodamia variegata*

The potential impacts of intraspecific and interspecific competition on fourth instars were evaluated using data

Table 1 Conspecific and allospecific combinations of eggs and fourth instars to evaluate intraguild predation and cannibalism

Combination	
1	Two *Eriopis connexa* larvae
2	Two *Hippodamia variegata* larvae
3	One *E. connexa* larva with one *H. variegata* larva
4	One *E. connexa* larva with *H. variegata* eggs
5	One *H. variegata* larva with *E. connexa* eggs
6	One *E. connexa* larva with *E. connexa* eggs
7	One *H. variegata* larva with *H. variegata* eggs

obtained from the IGP and cannibalism experiments described in the previous section. In a treatment where both larvae stayed alive in the presence of aphids (60 nymphs of *A. pisum*), voracity and body-weight change were assessed. For adults, one female of *E. connexa* or *H. variegata* along with one conspecific or allospecific female were kept for 24 h in the experimental setup previously described and provided with 40 aphids (20 per female, i.e., a number for which females of both species display similar levels of voracity, reproductive capacity and growth). All the adults used in this experiment were reared under the same conditions and were up to 15 days old. After 24 h, the voracity (see below), body weight, and reproductive capacity of females were recorded. To record changes in body weight of each individual, we marked one of the individuals with liquid paper to be able to identify it. In the replicates with two females of the same species, results for reproductive capacity were compared and presented per female. Fifteen replicates per treatment were conducted. The experiments were performed at 25 ± 1 °C, 75 ± 5% r.h, and L16:D8 photoperiod under fluorescent lamps. Two control treatments of 15 replicates each were performed in which a single female of *E. connexa* or *H. variegata* was kept alone in an experimental setup with 20 aphids.

In treatments with conspecifics, the voracity and fecundity of females was assumed to be equal. In allospecific treatments, the voracity of each female was estimated by the following methodology: (1) we summed the total number of aphids eaten by females in control treatments; (2) we calculated the proportion of total aphids eaten (rate of predation) by *E. connexa* or *H. variegata*; and (3) for each replicate, we multiplied the total voracity observed by the rate of predation. In allospecific treatments, eggs were separated and allowed to hatch to distinguish the species.

Statistical analysis compared voracity, changes in body weight and reproductive capacity of females of control treatments with those used within a conspecific or allospecific individual. One-factor ANOVA followed by Fisher's protected LSD test was used to compare voracity and mean changes in body weight. Due to the absence of normality in the data, log-linear analyses (with correction for overdispersion) modelling with the Genstat package were used to explore the relationship between the mean number of eggs per female, followed by a pairwise comparison test using SPSS. The proportion of ovipositing females was compared using the multiple comparison test for proportions, where significant results were those with a $q_{0.05,\infty,4}$ value >1.92 (Zar, 1996). All analyses were performed using SPSS 15.0 for Windows (SPSS, 2006).

Results

Fitness of *Eriopis connexa* and *Hippodamia variegata* females provided with different numbers of *Acyrthosiphon pisum*

For both ladybird beetle species, the number of prey eaten increased significantly with prey density (ANOVA: *H. variegata*: $F_{7,95}$ = 57.95; *E. connexa*: $F_{7,103}$ = 104.14, both P<0.05) (Figure 2). At each prey density, there were no significant differences in the number of aphids eaten by *E. connexa* and *H. variegata* (t-test: P>0.05).

The body weight of *H. variegata* females increased at all prey densities, with a non-significant decrease in the five-aphid treatment (ANOVA: $F_{7,95}$ = 1.65, P>0.05). *Eriopis connexa* displayed high individual variability in body-weight change. Although in this species, most differences were not significant, body-weight gain was lower at prey densities below 30 (ANOVA: $F_{7,103}$ = 2.09, P<0.05) (Figure 3).

Regarding the reproductive capacity for *H. variegata* females, we did not find significant differences in the number of clutches and eggs laid per female per day (ANOVA: $F_{2,36}$ = 0.65 and 0.70, P = 0.53 and 0.50, respectively) (Figure 4A and B). For *E. connexa* females, the reproduc-

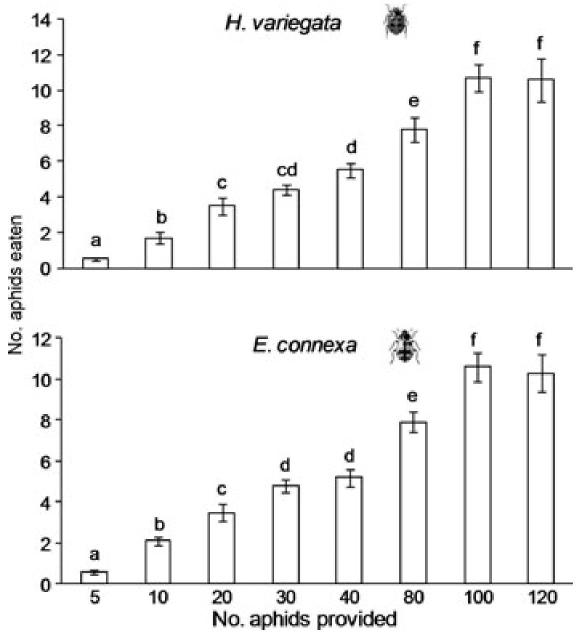

Figure 2 Mean (± SE) voracity (i.e., mean no. aphids eaten in 24 h) by *Hippodamia variegata* and *Eriopis connexa* females provided with different numbers of *Acyrthosiphon pisum*. Bars within a panel capped by the same letter are not significantly different (Fisher's protected least significant difference test: P>0.05).

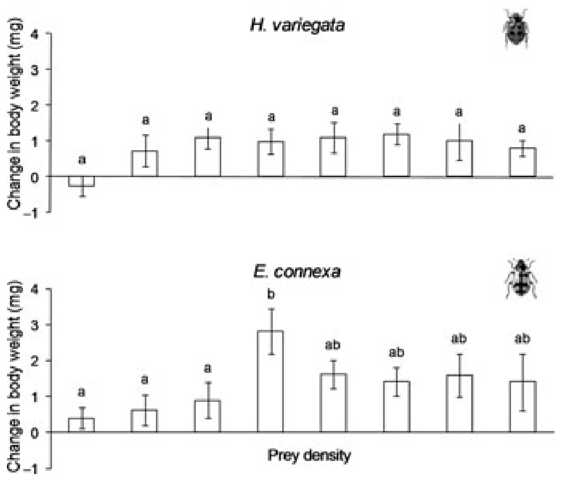

Figure 3 Mean (± SE) body weight of *Hippodamia variegata* and *Eriopis connexa* females after 3 days feeding at eight prey densities. Bars within a graph capped by the same letter are not significantly different (Fisher's protected least significant difference test: P>0.05).

tive capacity was significantly lower at prey densities of 5 and 20 aphids (number of clutches laid per female per day: ANOVA: $F_{2,42}$ = 5.22 and 6.39, P = 0.009 and 0.004, for number of clutches and eggs laid per female per day, respectively) (Figure 4C and D).

Intraguild predation and cannibalism

Intraguild predation exerted by *E. connexa* and *H. variegata* fourth instars on allospecific eggs did not differ significantly, either in absence or presence (both $F_{1,28}$ = 0.16, P = 0.69) of aphids (Figure 5A). There was no predation among larvae.

Cannibalism rates of *E. connexa* and *H. variegata* fourth instars on conspecific eggs did not differ significantly, either in absence or presence ($F_{1,28}$ = 2.15 and 0.0, P = 0.15 and 1.0, respectively) of aphids (Figure 5B). Cannibalism rates of *E. connexa* and *H. variegata* fourth instars on conspecific larvae did not differ significantly in absence of aphids ($F_{1,28}$ = 1.32, P = 0.26). There was no cannibalism among larvae in presence of aphids.

Competition between *Eriopis connexa* and *Hippodamia variegata*

In the experiments with larvae, *E. connexa* had significantly higher voracity in the presence of conspecific or allospecific larvae, but did not significantly change in body weight, whereas *H. variegata* did not significantly change in body weight or voracity in the presence of either conspecific or allospecific (Table 2). In the experiments with adults, we found that *E. connexa* significantly increased body weight and decreased reproductive capacity in competition with allospecifics. Fewer *E. connexa* laid eggs in the presence of other (mainly allospecific) females. The proportion of ovipositing *H. variegata* only decreased in presence of allospecifics (Table 3). In presence of conspecifics, *H. variegata*

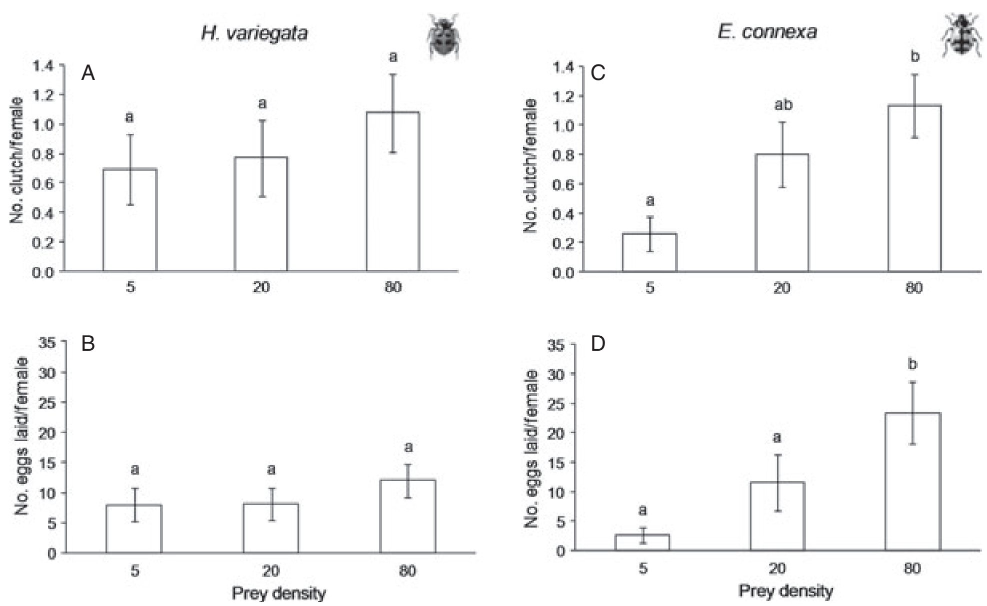

Figure 4 Daily reproductive capacity of *Hippodamia variegata* and *Eriopis connexa* females provided with three aphid densities. (A, C) Clutch size [mean (± SE) no. eggs per day per clutch] and (B, D) fecundity [mean (± SE) no. eggs per day per female]. Bars within a panel capped by the same letter are not significantly different (Fisher's protected least significant difference test: P>0.05).

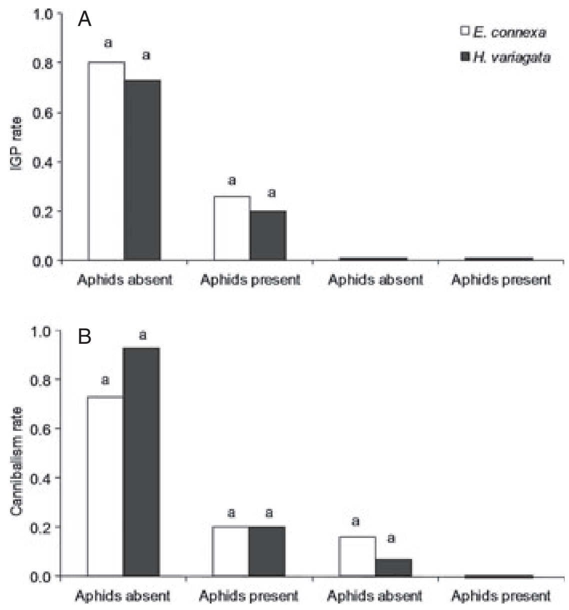

Figure 5 (A) Intraguild predation (IGP) rates and (B) cannibalism rates of fourth instars of *Eriopis connexa* and *Hippodamia variegata* on allospecific eggs or larvae in the absence or presence of aphids. The same letters within a treatment in both panels indicates no significant differences (logistic analysis corrected for overdispersion: P>0.05).

increased in voracity, but the other biological variables did not differ significantly (Table 3).

Discussion

We expected *H. variegata* to have higher fitness exploiting food resources than *E. connexa*. Both species displayed a similar voracity at each prey density, suggesting that the native and exotic ladybird beetles have similar foraging abilities within similar patches. Thus, neither has a potential intrinsic superiority in the exploitation of *A. pisum* in alfalfa fields. However, the allocation of aphid biomass to growth and reproduction differs between these species. Although *H. variegata* was able to maintain constant reproductive performance across the range of aphid densities tested, *E. connexa* exhibited decreased performance at lower aphid densities (5 and 20). This result suggests that *E. connexa* may be more sensitive and thus more responsive to a scarcity of resources. Within small prey patches, the native *E. connexa* concomitantly decreased body biomass and fecundity, whereas *H. variegata* preferentially allocated the ingested biomass to reproduction, keeping fecundity constant. Thus, it is expected that the native species may prefer to forage in large aphid colonies, whereas *H. variegata* may display a more ubiquitous presence over different prey patch sizes. These findings agree with field observations of the population dynamics of both aphids and predators that we have been performing since 1992 in central Chile (Grez, 1997). *Eriopis connexa* has its peak abundance in December (early summer), when aphids are abundant, whereas *H. variegata* peaks in January (mid-summer) and March, when aphids are scarce (Grez et al., 2004, 2005).

Intraguild predation and cannibalism are two important mortality factors among predators and they could be seen as regulatory mechanism of population growth, operating through a negative density-dependent feedback. Furthermore, IGP is frequently considered an important mechanism underlying the success of biological invasions. For instance, *H. axyridis* is a highly efficient intraguild predator and is also a very successful invader (Hironori & Katsuhiro, 1997; Yasuda & Ohnuma, 1999; Yasuda et al., 2001; Snyder et al., 2004; Brown et al., 2011; Evans et al., 2011). We predicted *H. variegata* to be a stronger IG predator than *E. connexa*, but our results do not support this prediction. Indeed, no IGP between fourth instars was

Table 2 Voracity (mean no. aphids eaten ± SE) and variation in body weight (mg ± SE) of fourth instars of *Eriopis connexa* and *Hippodamia variegata* in the presence of a conspecific or allospecific larva (n = 59)

	Control	Conspecific experiment[1]		Allospecific experiment	
Biological parameter	*E. connexa*	*E. connexa* 1	*E. connexa* 2	*E. connexa*	ANOVA
Voracity	3.7 ± 0.4a	5.1 ± 0.4b	5.1 ± 0.4b	3.9 ± 0.4a	$F_{3,59}$ = 3.23, P = 0.028
Variation in body weight	−0.24 ± 0.2a	0.06 ± 0.2a	0.013 ± 0.2a	0.22 ± 0.2a	$F_{3,59}$ = 0.71, P = 0.54
	H. variegata	*H. variegata* 1	*H. variegata* 2	*H. variegata*	
Voracity	4.8 ± 0.3a	5.3 ± 0.4a	5.3 ± 0.4a	5.1 ± 0.5a	$F_{3,59}$ = 0.28, P = 0.83
Variation in body weight	0.6 ± 0.2a	−0.3 ± 0.4a	0.92 ± 0.5a	0.5 ± 0.4a	$F_{3,59}$ = 1.70, P = 0.17

Means followed by different letters within a row are significantly different (Fisher's protected least significant difference test: P<0.05).
[1]Numbers 1 and 2 refer to the individuals tested.

Table 3 Voracity (mean no. aphids eaten ± SE), variation in body weight (mg ± SE), and reproductive performance of an adult *Eriopis connexa* and *Hippodamia variegata* female when alone and in the presence of a conspecific or allospecific adult (n = 59)

	Control	Conspecific experiment[1]		Allospecific experiment	ANOVA (F) or GLM (*F), or MCTP
Biological parameter	*E. connexa*	*E. connexa* 1	*E. connexa* 2	*E. connexa*	
Voracity	4.26 ± 0.53a	5.56 ± 0.37a	5.56 ± 0.37a	4.47 ± 0.5a	$F_{3,59}$ = 2.35, P = 0.081
Variation in body weight	−0.3 ± 0.2a	−0.04 ± 0.32a	0.26 ± 0.25a	1.24 ± 0.38b	$F_{3,59}$ = 5.1, P = 0.003
Proportion ovipositing females	0.4a	0.2b		0.06c	MCTP, P<0.05
No. eggs/female	4.1 ± 1.3a	1.2 ± 0.66b	1.2 ± 0.66b	0.4 ± 0.4b	*$F_{3,59}$ = 3.67, P = 0.018
	H. variegata	*H. variegata* 1	*H. variegata* 2	*H. variegata*	
Voracity	4.46 ± 0.29a	6.4 ± 0.5b	6.4 ± 0.5b	4.65 ± 0.52a	$F_{3,59}$ = 5.20, P = 0.002
Variation in body weight	0.05 ± 0.14a	1.18 ± 0.41a	0.74± 0.41a	0.85 ± 0.32a	$F_{3,59}$ = 1.9, P = 0.13
Proportion ovipositing females	0.4a	0.4a		0.06b	MCTP, P<0.05
No. eggs/female	4.1 ± 1.4a	1.93 ± 0.66a	1.93 ± 0.66a	0.4 ± 0.4a	*$F_{3,59}$ = 2.67, P = 0.057

Means followed by different letters within a row are significantly different (Fisher's protected least significant difference test: P<0.05).
MCTP, multiple comparison test for proportions.
[1]Numbers 1 and 2 refer to the individuals tested.

observed, and allospecific eggs were equally vulnerable to IGP. Lower relative abundance of *E. connexa* could be also related with a higher strength of cannibalism in the native compared with the exotic species. Once again, cannibalism rates of *E. connexa* and *H. variegata* on eggs did not differ significantly, either in the presence or absence of aphids. Moreover, the probability of occurrence of IGP did not differ significantly from that of cannibalism. One interesting result is the occurrence, in both species, of cannibalism among fourth instars in the absence of aphids, but not IGP, suggesting that, for larvae, cannibalism may be a more important mortality factor than IGP. All these results suggest that the regulatory mechanisms of population growth imposed by cannibalism and IGP may operate in a similar way, i.e., the negative effect of each species on the members of its own population is greater than its effect on the competitor.

The invasive ladybird beetle *H. axyridis* became dominant and replaced another exotic species, *C. septempunctata*, in the Midwestern, Pacific Northwest and Eastern states of the USA (LaMana & Miller, 1996; Brown & Miller, 1998). Apparently, *H. axyridis* affected the native arboreal ladybird beetle species, *Brachiacantha ursina* (Fabricius), *Cycloneda munda* (Say), and *Chilocorus stigma* (Say), in agricultural landscapes in south-western Michigan (Colunga-Garcia & Gage, 1998). In its native range, *H. axyridis* was dominant and replaced *C. septempunctata* in northern Japan when aphids became scarce (Hironori & Katsuhiro, 1997). Furthermore, competitive displacement of *Cycloneda sanguinea* (L.) from citrus ecosystems in Florida by *H. axyridis* has been reported (Michaud, 2002). If we assume that *E. connexa* and *H. variegata* are engaged in competition, they will expend some time and/or matter and/or energy on competition or its avoidance, thus reducing resources available for maintenance and reproduction (Krebs, 1994; Berryman & Kindlmann, 2008). Our results exhibited, in general, no significant differences in body weight or reproduction of *E. connexa* and *H. variegata* in experiments with either larvae or adults. In the experiments with conspecific larvae, *E. connexa* was able to increase voracity, but did not significantly change in body weight; it remains unclear as to why this happened. Also, we found a significant decrease in the number of eggs laid by the interacting *E. connexa* adults. However, this decrease was similar in conspecific and allospecific replicates. A significant result was the reduction in proportion of ovipositing females when an allospecific individual was present. A similar result was reported when reproductive performance of *C. undecimpunctata* females was affected by the presence of *H. axyridis*, but its body weight remained unaffected (Soares & Serpa, 2007). This result also suggests that, in the presence of allospecifics, resources were preferentially used for basal metabolism and body-weight maintenance, instead of reproduction. This situation could be advantageous for females, enabling them to use the biomass/energy in extensive search activities and, thus, to locate new patches in which the conditions are more advantageous for egg-laying and for their offspring. Once again, the mutual impact of *E. connexa* and *H. variegata* seems to be very similar.

Other mechanisms, such as chemical cues to habitat selection, may also be mediating the ecological interactions among these species. Indeed, olfactometry experiments have demonstrated that *E. connexa* avoids plants with conspecifics or with *H. variegata*, whereas *H. variegata* do not discriminate between plants with *E. connexa* or conspecifics (Tapia et al., 2010), suggesting a chemical-mediated antagonistic asymmetric interaction between these two species that favours *H. variegata* over *E. connexa*. This repellence may conduce to alteration of fitness, which is consistent with our finding of reduced oviposition of *E. connexa* in the presence of conspecific and allospecific.

The results obtained in our experiments suggest that the native and the exotic species were very similar in their biotic interactions. The impact of cannibalism, IGP and interspecific competition exerted by the species were very similar, and for this reason may not fully explain why *H. variegata* has increased its relative abundance in recent years. The higher sensitivity of *E. connexa* to prey patch size, along with other factors such as chemical-mediated negative intraspecific and interspecific interactions may be operating in alfalfa fields, changing the composition of coccinellid assemblages associated with this crop in Chile.

Acknowledgements

We thank Elizabeth Gazzano, Angélica Mancilla, and Francisca Morales for helping with the experiments. We also thank Ian Hardy for his helpful comments on statistical analyses, and Lidwien Raak-van den Berg, Peter Brown, and anonymous referees for their valuable suggestions on an earlier version of this paper. This study was supported by FONDECYT 1070412 and 7080091.

References

Alyokhin A & Sewell G (2004) Changes in a lady beetle community following the establishment of three alien species. Biological Invasions 6: 463–471.

Apablaza J & Stevenson T (1995) Fluctuaciones poblacionales de áfidos y de otros artrópodos en el follaje de alfalfa cultivada en la región metropolitana. Ciencia e Investigación Agraria 22: 115–121.

Berryman AA & Kindlmann P (2008) Population Systems: A General Introduction. Springer, Dordrecht, The Netherlands.

Brown MW & Miller SS (1998) Coccinellidae (Coleoptera) in apple orchards of eastern West Virginia and the impact of invasion by *Harmonia axyridis*. Entomological News 109: 143–151.

Brown PMJ, Thomas CE, Lombaert E, Jeffries DL, Estoup A & Handley LJL (2011) The global spread of *Harmonia axyridis* (Coleoptera: Coccinellidae): distribution, dispersal and routes of invasion. BioControl 56: 623–641.

Colunga-Garcia M & Gage SH (1998) Arrival, establishments and habitat use of the multicoloured Asian lady-beetle (Coleoptera: Coccinellidae) in the Michigan landscape. Environmental Entomology 27: 1574–1580.

Crowder DW & Snyder WE (2010) Eating their way to the top? Mechanisms underlying the success of invasive insect generalist predators. Biological Invasions 12: 2857–2876.

Elliot N, Kieckhefer R & Kauffman W (1996) Effects of an invading coccinellid on native coccinellids in an agricultural landscape. Oecologia 105: 537–544.

Evans EW (2000) Morphology of invasion: body size patterns associated with establishment of *Coccinella septempunctata* (Coleoptera: Coccinellidae) in western North America. European Journal of Entomology 97: 469–474.

Evans EW (2004) Habitat displacement of North American ladybirds by an introduced species. Ecology 85: 637–647.

Evans EW, Soares AO & Yasuda H (2011) Invasions by ladybugs, ladybirds, and other predatory beetles. BioControl 56: 597–611.

Félix S & Soares A (2004) Intraguild predation between the aphidophagous ladybird beetles *Harmonia axyridis* and *Coccinella undecimpunctata* (Coleoptera: Coccinellidae): the role of body weight. European Journal of Entomology 101: 237–242.

Grez AA (1997) Effect of habitat subdivision on the population dynamics of herbivorous and predatory insects. Revista Chilena de Historia Natural 70: 481–490.

Grez AA, Zaviezo T, Tischendorf L & Fahrig L (2004) A transient, positive effect of habitat fragmentation on insect population densities in experimental landscapes. Oecologia 141: 444–451.

Grez AA, Zaviezo T & Ríos M (2005) Ladybird (Coleoptera: Coccinellidae) dispersal in fragmented alfalfa landscapes. European Journal of Entomology 102: 209–216.

Grez AA, Zaviezo T, Díaz S, Camousseigt B & Cortés G (2008) Effects of habitat loss and fragmentation on the abundance and species richness of aphidophagous beetles and aphids in experimental alfalfa landscapes. European Journal of Entomology 105: 411–420.

Grez AA, Torres C, Zaviezo T, Lavandero B & Ramírez M (2010) Migration of coccinellids to alfalfa fields varying in adjacent vegetation in central Chile. Ciencia e Investigación Agraria 37: 111–121.

Hironori Y & Katsuhiro S (1997) Cannibalism and interspecific predation in two predatory ladybirds in relation to prey abundance in the field. Entomophaga 42: 153–163.

Hoffman W (1970) Die Gattung *Eriopis* Mulsant (Col. Coccinellidae). Mitteilungen der Münchner Entomologischen Gesellschaft 60: 102–116.

Hoogendoorn M & Heimpel G (2004) Competitive interaction between an exotic and native ladybeetle: a field cage study. Entomologia Experimentalis et Applicata 111: 19–28.

Kajita Y, Takano F, Yasuda H & Agarwala B (2000) Effects of indigenous ladybird species (Coleptera: Coccinellidae) on the survival of an exotic species in relation to prey abundance. Applied Entomology and Zoology 35: 473–479.

Koch AL (1974) Competitive coexistence of two predators utilizing the same prey under constant environmental conditions. Journal of Theoretical Biology 44: 387–395.

Krebs C (1994) Ecology. The Experimental Analysis of Distribution and Abundance, 4th edn. Addison-Wesley, San Francisco, CA, USA.

LaMana ML & Miller JC (1996) Field observation on *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) in Oregon. Biological Control 6: 232–237.

Lanzoni A, Accinelli G, Bazzocchi G & Burgio G (2004) Biological traits and life table of exotic *Harmonia axyridis* compared with *Hippodamia variegata*, and *Adalia bipunctata* (Col., Coccinellidae). Journal of Applied Entomology 128: 298–306.

Michaud JP (2002) Invasion of the Florida citrus ecosystem by *Harmonia axyridis* (Coleoptera: Coccinellidae) and asymmetric competition with a native species, *Cycloneda sanguinea*. Environmental Entomology 31: 827–835.

Mills N (2006) Interspecific competition among natural enemies and single versus multiple introductions in biological control. Trophic and Guild Interactions in Biological Control (ed. by J Brodeur & G Boivan), pp. 191–220. Springer, Dordrecht, The Netherlands.

Montes F (1970) Biología y morfología de *Eriopis connexa* Germar, 1824 y de *Adalia bipunctata* Linnaeus, 1758 (Coleoptera). Publicaciones del Centro de Estudios Entomológicos Universidad de Chile 10: 43–56.

Nóia M, Borges I & Soares A (2008) Intraguild predation between the aphidophagous ladybird beetles *Harmonia axyridis* and *Coccinella undecimpunctata* (Coleoptera: Coccinellidae): the role of intra and extraguild prey densities. Biological Control 46: 140–146.

Obrycki JJ, Giles KL & Ormond AM (1998) Interactions between an introduced and indigenous coccinellid species at different prey densities. Oecologia 117: 279–285.

Pimentel D, Lach L, Zúñiga R & Morrison D (2000) Environmental and economic costs of non-indigenous species in the United States. BioScience 50: 53–65.

Schellhorn NA & Andow DA (1999) Mortality of coccinellid (Coleoptera: Coccinellidae) larvae and pupae when prey become scarce. Environmental Entomology 28: 1092–1100.

Shigesada N & Kawasaki K (1997) Biological Invasions: Theory and Practice. Oxford University Press, Oxford, UK.

Simberloff D (1996) Risks of species introduced for biological control. Conservation Biology 78: 185–192.

Simberloff D & Stiling P (1996) How risky is biological control? Ecology 77: 1965–1974.

Snyder W, Clevenger G & Eigenbrode S (2004) Intraguild predation and successful invasion by introduced ladybird beetles. Oecologia 140: 559–565.

Soares A & Serpa A (2007) Interference competition between ladybird beetle adults (Coleoptera: Coccinellidae): effects on growth and reproductive capacity. Population Ecology 49: 37–43.

Soares AO, Coderre D & Schanderl H (2003) Effect of temperature and intraspecific allometry on predation by two phenotypes of *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae). Environmental Entomology 32: 939–944.

SPSS (2006) SPSS for Windows, Rel. 15.0.0. 2006. SPSS, Chicago, IL, USA.

Tapia DH, Morales F & Grez AA (2010) Olfactory cues mediating prey-searching behaviour in interacting aphidophagous predators: are semiochemicals key factors in predator-facilitation? Entomologia Experimentalis et Applicata 137: 28–35.

Turnock WJ, Wise IL & Matheson FO (2003) Abundance of some native coccinellines (Coleoptera: Coccinellidae) before and after the appearance of *Coccinella septempunctata*. Canadian Entomologist 135: 391–404.

Vitousek PM, Dantonio CM, Loope LL & Westbrooks R (1996) Biological invasions as global environmental change. American Scientist 84: 468–478.

Vitousek PM, Mooney HA, Lubchenco J & Melillo J (1997) Human domination of Earth's ecosystems. Science 277: 494–499.

Ware R, Yguel B & Majerus M (2009) Effects of competition, cannibalism and intraguild-predation on larval development of the European coccinellid *Adalia bipunctata* and the invasive species *Harmonia axyridis*. Ecological Entomology 34: 12–19.

Williamson M (1996) Biological Invasions. Chapman and Hall, London, UK.

Yasuda H & Ohnuma N (1999) Effect of cannibalism and predation on the larval performance of two ladybird beetles. Entomologia Experimetalis et Applicata 93: 63–67.

Yasuda H, Kikuchi T, Kindlmann P & Sato S (2001) Relationships between attack and escape rates, cannibalism, and intraguild predation in larvae of two predatory ladybirds. Journal of Insect Behavior 14: 373–384.

Yasuda H, Evans E, Kajita Y, Urakawa K & Takizawa T (2004) Asymmetric larval interaction between introduced and indigenous ladybird in North America. Oecologia 141: 722–731.

Zar JH (1996) Biostatistical Analysis. Prentice Hall, Upper Saddle River, NJ, USA.

Zaviezo T, Grez AA & Donoso D (2004) Dinámica temporal de coleópteros asociados a alfalfa. Ciencia e Investigación Agraria 31: 29–38.

Zaviezo T, Grez AA, Estades CF & Pérez A (2006) Effects of habitat loss, habitat fragmentation and isolation on the density, species richness and distribution of ladybeetles in manipulated alfalfa landscapes. Ecological Entomology 31: 646–656.