

Intraguild predation between an exotic and a native coccinellid in Argentina: the role of prey density

Luciana Mirande · Nicolas Desneux ·
Marina Haramboure · Marcela Inés Schneider

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Abstract *Harmonia axyridis* Pallas is a generalist predator native to Asia. It has been released both for classical and neoclassical biological control programs worldwide. Its presence has led to new ecological associations and it has been associated with the decline of indigenous natural enemies, notably ladybirds. These declines have been attributed to competition for resources and intraguild predation (IGP). *H. axyridis* was introduced in Argentina in 1986 to control the aphid *Myzus persicae*, although native coccinellid species are widespread in this area. *Eriopis connexa* Germar is the most abundant native coccinellid in Argentina. No study has assessed the possible ecological effects of the introduction of *H. axyridis* on naturally occurring aphid predators in Argentinian agro-ecosystems. This study evaluated IGP between *H. axyridis* and *E. connexa* at two different aphid densities under laboratory conditions. IGP occurred in 100 % of the cases when larvae of both species were reared together at low prey density and in 67 % of the cases at high prey density; at both prey levels, *H. axyridis* usually acted as the IG predator. The more rapid development to second and

third larval instars, larger body size, and more voracious behavior of *H. axyridis* compared to the native coccinellid could explain the IGP direction. This study showed the negative effect of *H. axyridis* on the native *E. connexa* under laboratory conditions, corroborated interactions between the species observed in field crops, and highlighted the impacts of this exotic predator on naturally occurring predator species.

Keywords *Harmonia axyridis* · *Eriopis connexa* · Neoclassical biological control · Invasive alien species · Resource competition

Introduction

The neoclassical biological control approach, which considers new species associations, is based on the ecological principle that a natural enemy that has not coevolved with a given pest could be more effective at controlling this pest (Pimentel et al. 1975; O'Connell et al. 2012). Controversy exists regarding this statement. Overall, several cases of successful biological control using both old and new associations have indicated a 75 % greater success rate if the predator/parasitoid and its prey/host are newly associated (Hokkanen and Pimentel 1984). However, new associations between exotic and local species in natural and agro-ecosystems may disrupt and destabilize species interactions (Heimpel et al. 2010; Ragsdale et al. 2011; Bompard et al. 2013; Jaworski et al. 2013). A new exotic predator could compete for a shared prey, causing niche overlap, and also interact directly with naturally occurring species through intraguild predation (IGP) (van Lenteren et al. 2003, 2006).

IGP occurs when two different species that share similar, potentially limiting resources (and therefore, may

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L. Mirande · M. Haramboure · M. I. Schneider (✉)
Centro de Estudios Parasitológicos y de Vectores [CEPAVE
(CONICET LA PLATA-UNLP)], Av. 120 s/n e/61 y 62,
La Plata CP 1900, Buenos Aires, Argentina
e-mail: mschneider@cepave.edu.ar

N. Desneux
French National Institute for Agricultural Research (INRA),
UMR1355-ISA, 400 Route des Chappes,
06903 Sophia-Antipolis, France

M. I. Schneider
Facultad de Ciencias Naturales y Museo, Universidad Nacional
de la Plata, Buenos Aires, Argentina

compete) interact trophically as well (Polis and McCormick 1989; Lucas et al. 1998; Chailleux et al. 2013; Velasco-Hernández et al. 2013; Moreno-Ripoll et al. 2014). The consumer species is named an intraguild predator or higher-order predator (IG predator), while the species suffering predation is the intraguild prey or intermediate-order predator (IG prey), and the common resource is the extraguild prey (Lucas et al. 1998). IGP has been documented in aphidophagous guilds (Agarwala and Dixon 1992; Phoofolo and Obrycki 1998; Ware et al. 2009; Gagnon et al. 2011a; 2011b), among which coccinellids represent important predators and are frequently involved in IGP interaction.

Harmonia axyridis (Pallas) (Coleoptera: Coccinellidae) is a coccinellid native to Asia (Hukusima and Kamei 1970) that is currently considered an invasive alien ladybird in North America (Gordon 1985; Coderre et al. 1995; Hesler et al. 2001), Europe (Ipertti and Bertand 2001; Majerus et al. 2006; Brown et al. 2008), and Africa (Brown et al. 2011), where it was widely introduced as a biological control agent of aphids. In Argentina, *H. axyridis*, was introduced in 1986 in the province of Mendoza from France as part of a neoclassical biological control program against the aphid *Myzus persicae* Schultz (Hemiptera: Aphididae) (García et al. 1999). It spread rapidly and was detected in the province of Buenos Aires in 2001 (Saini 2004). It has also been reported from other South American countries (Almeida and da Silva 2002; Grez et al. 2010; Brown et al. 2011).

Argentinian agro-ecosystems have various coccinellid species, most of which are native. Among these species, *Eriopis connexa* (Germar) is widely distributed throughout the Neotropical Region in vegetable and fruit crops (Duarte Gómez and Zenner de Polanía 2009). It is a generalist predator of several potential phytophagous pests, such as aphids (Sarmiento et al. 2004) and other soft-bodied pests (Lepidoptera, spider mites, etc.). It was released in the United States to control the Russian wheat aphid *Diuraphis noxia* (Mordvilko) (Reed and Pike 1991).

In South America, *E. connexa* limits populations of *M. persicae* (Sulzer) and *Macrosiphum euphorbiae* (Thomas) in Chile (Quiroz et al. 2005), and it has been cited as an important predator of *Myzus nicotianae* (Blackman) and *M. persicae* in Argentina (Ohashi and Urdampilleta 2003). It predates on *Rachiplusia nu* (Gueneé) and *Pseudoplusia includens* (Walker) (Noctuidae) in Brazil (Rocha de Moraes et al. 1991), where it is considered an excellent potential biological control agent (Almeida Sarmiento et al. 2007; Silva et al. 2013).

Harmonia axyridis has been studied both within its native guild and within exotic guilds where it has established as an invasive alien. It can have strong negative effects not only on the diversity of other natural enemies of

aphids but also on biodiversity more widely (Pell et al. 2008; Michaud 2012). This species is an efficient interspecific competitor, and it has adversely impacted a wide range of indigenous coccinellids (Michaud 2002; Cottrell 2004; Koch et al. 2006; Alhmedi et al. 2010) and other aphidophagous predators (Phoofolo and Obrycki 1998; Ingels and De Clercq 2011) through both food resource competition and IGP interaction.

In field studies, we have observed *H. axyridis* larvae preying on *E. connexa* larvae in artichoke crops with high aphid population levels (Mirande L., unpublished data). Therefore, we hypothesize that *H. axyridis*, since its introduction into Argentina, may negatively affect native coccinellid populations through IGP. Such IGP by *H. axyridis* may ultimately impact on the natural biocontrol of phytophagous pests by coccinellids. Thus, the aim of this study was to evaluate, under laboratory conditions, the occurrence of IGP between *H. axyridis* and *E. connexa* at two aphid prey densities. Developmental time and pupal weight were recorded as indicators of the magnitude of interactions between the species.

Materials and methods

The ladybird rearing and experiments were carried out in climatic chambers at 25 ± 0.5 °C, 75 ± 5 % relative humidity and a 16:8 L:D photoperiod.

Insects and plant material

The coccinellids *H. axyridis* and *E. connexa* were collected from vegetable crops in La Plata region (an important horticultural area in Argentina; 34.9°S, 57.8°W). The samplings were generally done at least 20 day after spraying dates, which were generally based on pest monitoring. In the laboratory, the beetles were conditioned in ventilated plastic containers (15 cm diameter, 9 cm high) covered with a fine mesh and quarantined to minimize parasitism and disease. The progeny of this field material was used to initiate the laboratory colonies of both species.

The prey *Rhopalosiphum padi* L. (Hemiptera: Aphididae) was obtained from clones supplied by Faculty of Agronomic and Forest Sciences (National University of La Plata, Buenos Aires Argentina), and they were reared on *Triticum aestivum* L. cv. ACA 901 seedlings. Seeds of *T. aestivum* were germinated in plastic pots (6 cm high, and 6 cm diameter) with standard substrate (fertile soil and perlite 1:1 v/v) and infested with aphids at germination. The seedlings were conditioned and maintained in ventilated plastic boxes (13 cm high × 30 cm long × 23 cm wide) until more than 80 % of each seedling was infested with aphids.

Coccinellid species were fed on prey ad libitum and a new artificial diet developed in our laboratory (Schneider MI, unpublished data) and raisins were added as nutritional supplements. Young adults from colonies were maintained under these same conditions until mating (5 day for *E. connexa*, 7 day for *H. axyridis*, according to preliminary studies). Afterward, groups of five females of each species were randomly selected and isolated; their egg clusters were collected daily and placed in a 6-cm diameter Petri dish until the eggs hatched.

Bioassays: single predator vs. IGP trials

Ladybird neonates (within 24 h of hatching) of *H. axyridis* and *E. connexa* were randomly selected from cohorts and used for the bioassays. They were placed in ventilated arenas (8 cm high, 6 cm diameter) using a fine brush. Three treatments were carried out with each coccinellid species separately and together (single vs. interaction) at two different aphid prey densities (low and high) for a total of six treatments. Prey density was based on pilot experiments (Mirande L, unpublished data) on the nutritional requirements for the development of the coccinellid larval instars. The low prey density corresponded to the minimal number of aphids sufficient for both coccinellid species to complete their life cycles. The high prey density was three times this amount. In the interaction treatments, twice the number of aphids was supplied per arena as in the individual treatments. The treatments were replicated 20–22 times and are detailed below.

Single predator trial

This treatment was a control to record the natural mortality of each species. Each arena contained one first larval instar (immediately after hatching). Besides, the role of prey density was assessed. One group of arenas was supplied with a low aphid prey density (10, 20, 30, and 40 aphids per day for the 1st, 2nd, 3rd, and 4th instar, respectively) and the other group with a high prey density (30, 60, 90, and 120 aphids per day for the 1st, 2nd, 3rd, and 4th instar, respectively).

IGP trial

Two first instars, one of each species, were placed together in the arenas. Prey density provided was twice of that supplied in the individual trials. At low prey density, 20, 40, 60, and 80 aphids were supplied for the 1st, 2nd, 3rd, and 4th instars, respectively; whereas at high prey density the aphid numbers were 60, 120, 180, and 240 aphids, respectively. If one of the predator larvae was eaten, the number of aphids supplied per arena was adjusted to a

single predator trial. Pleated paper (to mimic foliage) was added as refuges to the arenas.

Coccinellid survival was checked daily until adult emergence. In addition, the duration of each instar and the pupal stage was recorded. Finally, pupal weight was measured using an analytical balance (Acculab[®]) with a precision of 10^{-4} g to record size differences between *H. axyridis* and *E. connexa*, and to relate this size difference with any observed IGP. The weight variation (VP_w) for both species from the single to IGP condition was estimated as

$$VP_w = (P_wIGP - \bar{X}P_wS) \div \bar{X}P_wS \times 100,$$

where P_wIGP is the pupal weight of the predator in the IGP trial, and $\bar{X}P_wS$ is the pupal weight mean in the single trial. A negative value of VP_w was considered a weight reduction.

Statistical analysis

The proportion of coccinellids found alive at each development stage (i.e., survival), in the single predator and IGP trials, was analyzed using a log-linear model (proc genmod in SAS, SAS Institute, Cary, NC, USA) where sources of variation were: coccinellid species '*Species*' (*H. axyridis* and *E. connexa*), predator stage '*Stage*' (first, second, third, fourth larval instars, and pupa and adult stages), and aphid density '*Prey density*' (low and high aphid densities).

To test for differences in instar duration time and pupal weight, analysis of variance (ANOVA) was used after log-transforming the data ($\log(x + 1)$) when necessary to ensure normality and homoscedasticity of variances. Means were separated using Fisher's least significant difference test (Scheiner and Gurevitch, 2001). When ANOVA assumptions were not met, a Kruskal–Wallis test was used. These analyses were performed using Statgraphic v. 4 (STSC, 1987). In all tests, $P \leq 0.05$ was considered significant.

Results

Survival assessment

The statistical results of the log-linear model analysis are summarized in Table 1. When the coccinellids were tested in the single predator conditions, mortality did not differ significantly between species ("Species" factor not significant, Fig. 1A). However, it was not distributed equally among developmental stages (significant "Stage" factor). This mortality pattern occurred similarly in both species (no significant "Stage" \times "Species" interaction). Early larval stages (2nd and 3rd instars) of both species were more likely

to die than older ones (e.g., 4th instars). Prey density (low vs. high) also had a significant effect on survival (significant “Prey density” factor) that was similar in both coccinellids

Table 1 Statistics from the log-linear model used to analyze the survival of coccinellids when tested in (A) single predator or (B) intraguild predation (IGP) conditions

Source of variation	Degrees of freedom	F	P value
(A) Single predator condition			
Species	1	1.74	0.187
Stage	1	3.93	0.047
Prey density	5	11.65	0.040
Species × stage	1	2.67	0.102
Species × prey density	5	9.09	0.105
Prey density × stage	5	1.14	0.950
(B) IGP condition			
Species	1	36.89	<0.01
Stage	1	3.76	0.052
Prey density	5	39.79	<0.01
Species × stage	1	1.31	0.252
Species × prey density	5	16.61	0.025
Prey density × stage	5	11.06	0.050

Survival was evaluated as functions of coccinellid species (“species” factor), predator stage (“stage”), and aphid density (“prey density”)

species when tested as single predators (no significant “Prey density” × “Species” interaction). Low prey density reduced survival up to 25 % in both coccinellid species, regardless of coccinellid development stage (no significant “Prey density” × “Stage” interaction).

When the two coccinellids were tested in the IGP conditions, survival of *E. connexa* and *H. axyridis* differed significantly (significant “Species” factor, Fig. 1B). *H. axyridis* acted as the IG predator in most cases, as reflected in the drastic reduction in survival of *E. connexa* (55.29–81.33 %), while *H. axyridis* mortality always remained below 20 %. Mortality may depend on coccinellid instar (“Stage”) in the IGP conditions, though it was nearly significant ($P = 0.052$) in our study and was similar in the two coccinellids species (no significant “Stage” × “Species” interaction). Prey density had a strong effect on coccinellid survival (significant “Prey density” factor). IGP occurred in 100 % of the cases at low prey density and in 67 % at high prey density. However, prey density did not affect *E. connexa* and *H. axyridis* survival in the same way (significant “Species” × “Prey density” interaction). Finally, the impact of prey density on coccinellid survival in the IGP trials was not equal among the stages; i.e., some stages were at higher risk of predation than others at low prey density (marginally significant “Stage” × “Prey density” interaction).

Fig. 1 Survival of *Harmonia axyridis* and *Eriopis connexa* at different development stages reared alone (A) and under intraguild predation (IGP) conditions (B) at low prey density (LPD) and high prey density (HPD). Data correspond to the proportion of survivors having into account the organisms dead

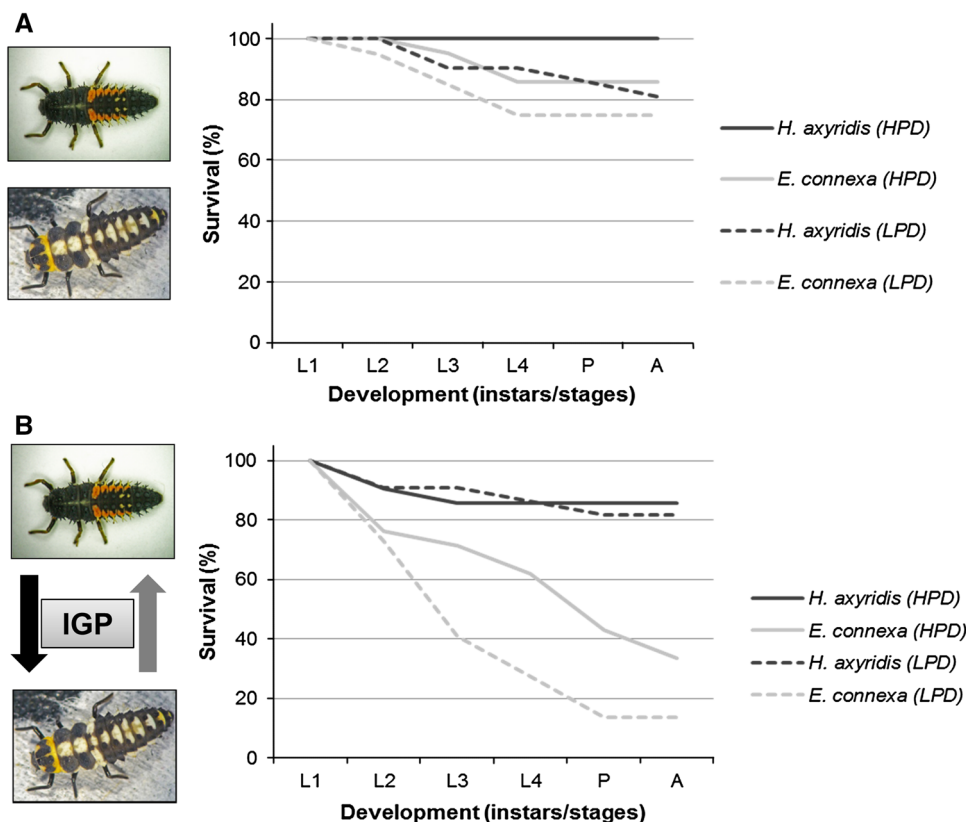
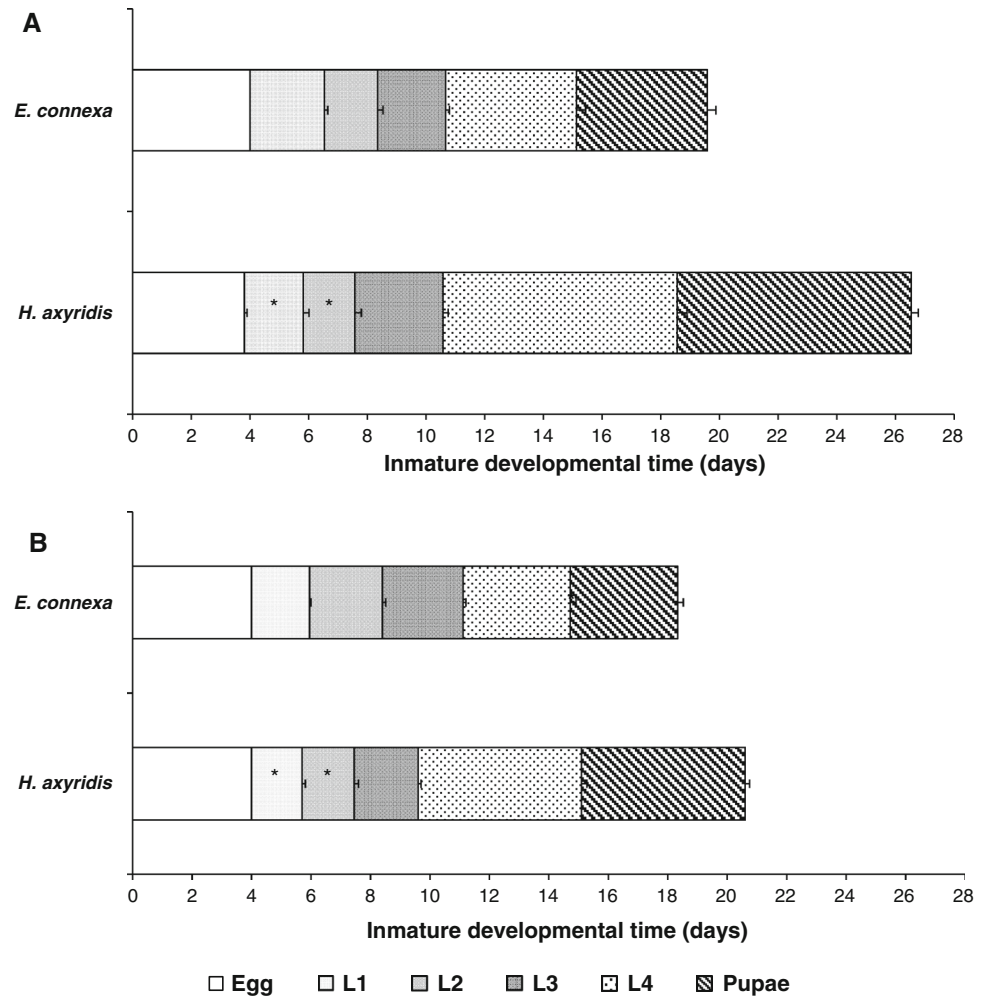


Fig. 2 Immature development time (egg to pupa) of *Harmonia axyridis* and *Eriopis connexa* reared alone at low (A) and high prey density (B). Asterisk denotes significant differences between species. Data are means \pm SE



Developmental time (single predator trial)

Eriopis connexa reached the pupal and adult stages earlier than *H. axyridis* at both prey densities, but the effect was stronger at low prey density. The native coccinellid reached the two stages 3.44 and 3.60 days earlier than the Asian ladybird at low prey density (pupal stage: $F = 54.83$; $df = 1, 31$; $P < 0.001$; adult stage: $F = 86.98$; $df = 1, 30$; $P < 0.001$). Moreover, *E. connexa* completed its life cycle (from egg to adult) in 19 and 17.33 days at low and high prey density, respectively, whereas *H. axyridis* required 22.67 and 19.65 days, respectively. However, *H. axyridis* reached the second and third larvae instars earlier than *E. connexa* at both prey densities evaluated (second instar: $H = 9.57$, $P = 0.002$ at low prey density; $H = 4.49$, $P = 0.034$ at high density; third instar: $F = 6.89$, $df = 1, 34$, $P = 0.013$ for low density; and $F = 24.94$, $df = 1, 38$, $P < 0.001$ for high density; Fig. 2).

Pupal weight (single predator vs. IGP trial)

Although the pupal weight of both coccinellid species was related to the amount of prey provided, the actual biological characteristics of each species also affected weight variation in the single predator and IGP conditions. In single predator condition, *H. axyridis* pupal weight was 48.1 % higher when they were provided with high density aphid prey as opposed to low density. In contrast, the pupal weight of the native coccinellid was only 23.9 % higher at high aphid density compared with low prey density (Fig. 3A). In the IGP condition, *H. axyridis* weighed 67 % more when the prey density increased, while *E. connexa* did not increase its pupal weight even at high prey density (Fig. 3B).

In addition, weight variation in both coccinellid species between single and intraguild predation conditions was analyzed. In IGP trials, *H. axyridis* pupae weighed 27.41 % more at high prey density, whereas *E. connexa* increased around 10.9 % at low prey density (Fig. 3C).

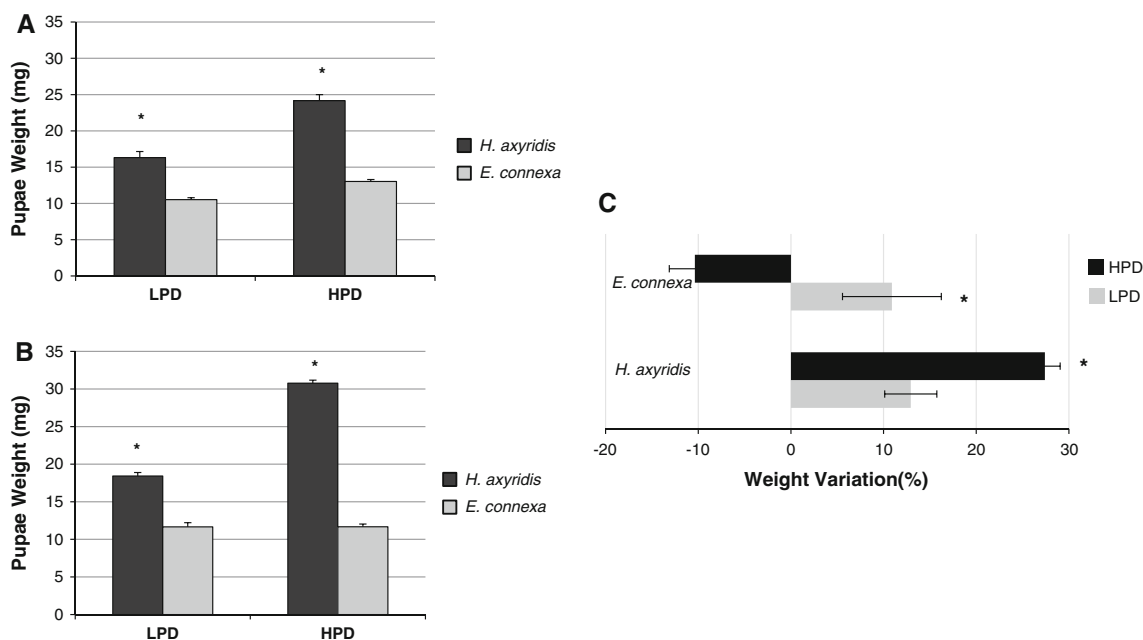


Fig. 3 Pupal weight of *Harmonia axyridis* and *Eriopis connexa* reared under single predator (A) and intraguilid predation (IGP) conditions (B) at low prey density (LPD) and high prey density (HPD). Pupal weight variation between single predator and IGP conditions at both prey densities (C). Data are means \pm SE. ANOVA

was used. Asterisk denotes significant differences. a: *H. axyridis* $F = 43.85$; $df = 1, 36$; $P < 0.001$; *E. connexa* $F = 43.13$; $df = 1, 31$; $P < 0.001$; b: *H. axyridis* $F = 413.32$; $df = 1, 34$; $P < 0.001$; *E. connexa* $F = 0.00$; $df = 1, 10$; $P < 0.99$; c: *H. axyridis* $F = 19.70$; $df = 1, 34$; $P < 0.001$; *E. connexa* $F = 14.14$; $df = 1, 10$; $P < 0.001$

Discussion

The status of *H. axyridis* as an invasive species has been documented (Roy and Wajnberg 2008). The negative effect on native coccinellid species from its introduction for classical or neoclassical biological pest control has been noted in several countries, notably in the Palearctic region, but it has been poorly documented in Neotropical areas. This impact worldwide is mainly due to IGP interactions in which the exotic species is the intraguilid predator (Koch et al. 2006). *H. axyridis* was introduced into Argentina in 1996 to control *M. persicae*, but the environmental risks of its releases have not been documented yet. Therefore, potential IGP between larvae of the exotic *H. axyridis* and the native *E. connexa* was characterized under laboratory conditions.

Our study corroborated the occurrence of IGP between *H. axyridis* and *E. connexa* at two prey densities. Several authors have also noted that the density of the extraguilid prey can affect the occurrence and strength of IGP (Lucas et al. 1998; Obyrcki et al. 1998). In this case, the direction of IGP remained constant with *H. axyridis* as the IG predator, regardless of the extraguilid prey density. In addition, these results are consistent with other studies in which *H. axyridis* showed a lower rate of IGP when higher densities of extraguilid prey were supplied (Nóia et al. 2008; Sato et al. 2008).

In field conditions, a mixture of cohorts of both predators coexist and a number of encounters of different developmental stages occur (Mirande L., unpublished data), probably most of them are involved in IGP. The present study represents in laboratory conditions, some of those possible scenarios, in which cohorts of both species of the same age coincide at different prey levels. The Asian ladybird developed to second and third instars earlier than the native one at both prey densities. This fact may be another advantage for *H. axyridis* and could influence the direction of IGP, with older *H. axyridis* larvae eating younger *E. connexa* ones. Our results were consistent with reports by Lucas et al. (1998) and Yasuda et al. (2004) who reported that early instars, which are the smallest individuals, were particularly vulnerable to predation.

Body size is a relevant factor that could affect IGP; generally larger individuals feed on smaller ones (Cottrell and Yeorgan 1998; Lucas et al. 1998). Although the larval size of these two species was not analyzed in this study, it may be strongly linked to pupal weight. Pupae of *H. axyridis* were heavier than those of *E. connexa*, corroborating that the introduced species is larger than the native one. The higher weight of the Asian ladybird may enhance its IG predator role.

The large size of *H. axyridis* could be related to its voracity. We have observed that it efficiently used available prey for its own benefit, whereas the native coccinellid

was not able to increase its weight when prey density increased. Harmon et al. (2007) highlighted that competition for resources is an important mechanism by which *H. axyridis* could displace native coccinellids, independent of IGP. Laboratory studies have documented the more aggressive behavior of this invasive ladybird's larvae than those of other coccinellids; *H. axyridis* find aphid prey more quickly than other ladybirds (Yasuda et al. 2001; Félix and Soares 2004). Thus, *H. axyridis* increased its predatory capacity when the prey density increased in single predator and IGP conditions, although the effect was higher under IGP.

In conclusion, IGP could displace native species in regions invaded by *H. axyridis*, which appears to be a top predator in the guild of aphidophagous insects (Koch 2003). Our work provides new information on the possible negative impacts of *H. axyridis* in South America and is consistent with previous studies showing the negative effects of *H. axyridis* on indigenous coccinellids in North America and Europe (Coderre et al. 1995; Cottrell 2004; Yasuda et al. 2004; Moser and Obrycki 2009; Hautier et al. 2011). The present study illustrates some of the mechanisms through which the predation of native coccinellids by Asian ladybird larvae observed in the field (Mirande L., unpublished data) may significantly affect native ladybird populations. Our laboratory results suggest that prey density, coccinellid size, and development stage could play an important part in the IGP interactions between the species evaluated.

Further studies should be addressed including other South American coccinellid species to complete the environmental risks evaluation of this exotic invasive species. Such studies could be useful to establish regulation guidelines for *H. axyridis* dispersion to reduce its negative impact on other predators.

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