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ORIGINAL ARTICLE

Stage-specific vulnerability of *Harmonia axyridis* (Coleoptera: Coccinellidae) to intraguild predation*

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Abstract. The multicoloured Asian ladybeetle, *Harmonia axyridis* (Pallas), is a widespread invasive ladybird. It is considered a top predator among the aphidophagous coccinellids in North America and Europe; thus, it is supposed to be free from predation pressure by other members of the guild. Our study aims to evaluate the stage-specific vulnerability of *H. axyridis* to intraguild predation (IGP) by the indigenous *Coleomegilla maculata lengi* Timberlake and the invasive *Propylea quatuordecimpunctata* Linnaeus. We hypothesised that (1) *H. axyridis* stages will be less susceptible to IGP than the two other species, (2) vulnerability to IGP will decrease with the age of the larvae and (3) vulnerability to IGP will increase with increased weight difference between intraguild predator (IGPredator) and intraguild prey (IGPrey). Eggs, 1st and 2nd instars of *H. axyridis* were susceptible to IGP by both *C. maculata* and *P. quatuordecimpunctata* adults and larvae, but less vulnerable than the other beetles when facing the same IGPredator. Vulnerability to IGP for the three species was reduced with increased age of larvae and with decreased weight difference. Overall, *H. axyridis* was less vulnerable to IGP than the two other species, but the results confirm the fact that the status of IGPrey or IGPredator of *H. axyridis* will be determined by the stages of both species during the interactions.

1. INTRODUCTION

The Coccinellidae family includes approximately 6000 different species (Nedvěd & Kovář, 2012), comprising many important biological control agents of agricultural pests (De Bach, 1964; Iperti, 1999; Michaud, 2012). During the last century, the trade of such helpful species has been of major concern for implementing more sustainable pest control strategies (Gordon, 1985). In some cases, introduced ladybeetles rapidly established and spread throughout the non-native territory, leading to serious invasions with major consequences on native species (Michaud, 2012; Roy et al., 2012), mainly as a result of intraguild interactions (Hautier et al., 2011; Bahlai et al., 2014). Among these interactions, intraguild predation (IGP: predation event where a member of the guild preys upon another member of the same guild; Lucas & Maisonhaute, 2019) by invasive coccinellids has been reported as quite common in the field (Hautier et al., 2011; Thomas et al., 2012), and even at high prey densities (Gardiner & Landis, 2007; Mirande et al., 2015). It represents an adaptive value, providing the intraguild predator (IGPredator) with significant benefits, such as the elimination of a competitor or a potential predator, consumption of a protein-rich meal (Polis et al., 1989) and acquisition of toxins from intraguild prey (IGPrey) (Hautier et al., 2008, Lucas et al., 2012); however, IGP detrimental effects, such as changes in ladybeetle species diversity (Lucas et al., 2007; Grez et al., 2016) and biological control disruption (Michaud, 2012) have already been reported.

The multicoloured Asian ladybeetle, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), is an East-Palearctic species native to Japan, China, Korea, Mongolia and Siberia (Koch, 2003). This species was introduced to America and Europe in the late 1980s and the early 2000s, respectively, for aphid biological control purposes (Sloggett & Honek, 2012), where it rapidly became established and then invasive, leading to a well-documented disruption of native ladybird assemblages (Roy et al., 2012; Grez et al., 2016; Meseguer et al., 2022). There is a strong agreement that *H. axyridis* is a top predator (Majerus et al., 2006;

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Ware & Majerus, 2008; but see Soares et al., 2008). A top predator is considered to be free from predation pressure and its populations are more regulated by bottom-up than top-down effects (Gittleman & Gomper, 2005). The ability of *H. axyridis* to perform IGP explains in part its status (Ware & Majerus, 2008; Hautier et al., 2011; Katsanis et al., 2013). However, to be a top predator, animals need to be dominant in the guild, and almost invulnerable to predation at all life stages. This concept needs to be questioned for insects. They go through multiple juvenile stages, called instars, experiencing drastic differences in size and defensive abilities, and through multiple moults, where they may be highly vulnerable to predation unless they have some physical, biological, chemical, physiological, or behavioural protection (Lucas et al., 2000; Greeney et al., 2012 Vilcinskas et al., 2013; Pacheco et al., 2021).

Numerous studies, mainly in the laboratory, confirm that *H. axyridis* dominates IGP confrontations with a great number of coccinellid species, such as *Adalia bipunctata* Linnaeus (Hautier et al., 2010), *Coccinella septempunctata* Linnaeus (Yasuda et al., 2001; Ware & Majerus, 2008; Raak-van den Berg et al., 2012), *Coccinella transversoguttata* Falderman (Snyder et al., 2004; Yasuda et al., 2004) *Coccinella undecimpunctata* Linnaeus (Félix & Soares, 2004; Nóia et al., 2008), *Olla v-nigrum* Mulsant (Michaud & Grant, 2003; Cottrell, 2004, 2007), *Cycloneda sanguinea* Linnaeus (Michaud, 2002), *Propylea japonica* Linnaeus (Ware & Majerus, 2008), *Coleomegilla maculata* DeGeer (Cottrell & Yeargan, 1998; Cottrell, 2004, 2007), *Cycloneda munda* Say (Cottrell, 2007) and *Hippodamia convergens* Guérin-Meneville (Snyder et al., 2004; Yasuda et al., 2004; Cottrell, 2007). Other non-coccinellids species are also IGPrey for *H. axyridis*, such as lacewings (Michaud & Grant, 2003; Gardiner & Landis, 2007; Wells et al., 2017), mirids (Provost et al., 2005) or the cecidomyiid *Aphidoletes aphidimyza* (Rondani) (Gardiner & Landis, 2007; Voynaud, 2008). Nevertheless, some studies report *H. axyridis* becoming an IGprey (Ware & Majerus, 2008). Cottrell & Yeargan (1998) reported successful predation of *C. maculata* 3rd and 4th instars on 1st and 3rd instars of *H. axyridis*, respectively. Eggs of *H. axyridis* also seem vulnerable to predation, but most species experience a high level of mortality when fed with eggs of this species (Sato & Dixon, 2004; Cottrell, 2004, 2007). *Harmonia axyridis* is also attacked by other species, such as chrysopid (Nedvěd et al., 2013) and hemipteran species (De Clercq et al., 2003; Ceryngier et al., 2018; Labrie et al., unpubl. data) or spiders (Yasuda & Kimura, 2001; Ceryngier et al., 2018).

Susceptibility to IGP is driven by many factors. All traits determining the stage reached by an individual ladybeetle at the time of the intraguild interaction, such as time of colonisation, life cycle length, voltinism, etc., could influence the probability, type, and outcome of the interaction (Lucas, 2012). Environmental characteristics, such as spatial scales of investigation (laboratory vs field experiments), human activity (use of pesticides), food availability, or presence of refuges, could also reduce or enhance susceptibility to IGP (Lucas, 2005; Lucas & Maisonhaute, 2019; De Donder et al., 2022). Plants or microhabitats on plants may provide refuges for the IGPrey or may reduce predator mobility (Lucas & Brodeur, 1999; Lucas et al., 2000; Riddick et al., 2014). Mobility of the IGPrey (Lucas et al., 1998, Lucas, 2005) and efficient escape behaviour (Yasuda et al., 2001; Pell et al., 2008) could also reduce IGP. Immobile stages, such as eggs or pupae are highly vulnerable to IGP, so the selection of secure egg-laying and pupating sites seems crucial to counteract this lack of mobility (Lucas et al., 2000; Pérez-Rodríguez & Messelink, 2022). The occurrence of IGP is also highly correlated to body size difference between the protagonists (Lucas, 2012). Coccinellids and competitors experience at least a 10-fold increase in body size during their immature development. Thus, an encounter between small, less mobile, less defended, early instars or eggs, with larger, more mobile, more powerful, late instars or adults, can result in antagonistic interactions (Lucas et al., 1998; Félix & Soares, 2004; Lucas, 2012). Priority effect, which implies that the time of arrival during the season will determine the outcome of the dominance of a species in a habitat, can also influence the outcome of IGP (Morin, 1999; Rasmussen et al., 2014). For example, larvae of a smaller predator species could be larger than larvae of a co-occurring larger predator species at a specific moment, and this may reverse the direction of the IGP (Lucas, 2005).

Our study aims to evaluate the stage-specific vulnerability of *H. axyridis* to IGP by the indigenous *C. maculata* and the invasive *Propylea quatuordecimpunctata* L. for all combinations. All three species overlap temporally and are regularly found on the same plant/aphid system (maize, wheat, potato, goldenrods, milkweeds…) in Eastern Canada (Lucas et al., 2007). *Coleomegilla maculata* is considered as one of the most polyphagous ladybeetles, being able to develop both on plant and animal material (aphids, mites, immature stages of lepidopteran and coleopteran species, whiteflies…) (Musser & Shelton, 2003; Michaud & Grant, 2005), whereas *P. quatuordecimpunctata*'s diet range is more restricted, being mostly aphidophagous (Kalushkov & Hodek, 2005).

Vulnerability assessment in Coccinellidae has always been done by comparing the vulnerability of the first species to the other one, but to compare the susceptibility of two species, it has to be done by comparing both species when facing a third one. As previously stated, a top predator needs to be dominant in the guild, and almost invulnerable to predation by other species. We hypothesised that (1) *H. axyridis* stages will be less susceptible to IGP than the two other species when facing the same IGPredator, (2) vulnerability to IGP will decrease with the age of the larvae, and (3) intensity and direction of IGP will be determined by relative body weight difference between IGPredator and IGPrey.

2. MATERIALS AND METHODS

Experiments were carried out in the laboratory to evaluate the intensity, direction and symmetry of IGP between all developmental stages (eggs, four larval instars, pupae, and adults) of *H.*

axyridis, *C. maculata* and *P. quatuordecimpunctata*, as well as their vulnerability to IGP. Adults of the three ladybird species were manually collected in the borders of different wheat, maize and soybean fields in Sherington (45°09′59″, 73°31′32″) and St-Hyacinthe (45°37′00″, 72°57′00″) regions (Quebec, Canada) in 2001. Adults were kept in the laboratory and reared inside plastic framed cages (35 × 35 × 35 cm) covered by muslin. To avoid food adaptation, they were fed on a mixed diet of the black bean aphid, *Aphis fabae* Scopoli (Hemiptera: Aphididae), commercial crushed pollen, and eggs of *Sitotroga cerealella* (Olivier, 1789) (Lepidoptera: Gelechiidae) at 24 ± 1°C, 75% ± 5% RH and a light regime of 16L : 8D photoperiod. Eggs of each species were then separated individually and incubated at the abovementioned constant conditions for larval development. Experimental individuals at the required life stage were removed when needed. Prior to the beginning of the tests, all individuals were starved for 24h and then weighed using a Mettler AM 50 analytical balance with a precision of ± 0.1 mg. All tests were performed at 24 ± 1°C, 75% ± 5% RH and a light regime of 16L : 8D photoperiod.

2.1. IGP between *H. axyridis*, *C. maculata* and *P. quatuordecimpunctata*

IGP experiments were performed in Petri dishes of 50 mm × 9.4 mm containing moist cotton rolls to keep humidity constant. Experimental pairings, consisting of one individual of each species, were placed in one Petri dish for 24 h. This design was replicated 15 times for each combination of stages for the three species (*H. axyridis* vs *C. maculata*, *H. axyridis* vs *P. quatuordecimpunctata* and *P. quatuordecimpunctata* vs *C. maculata*). Five eggs were provided in the combinations that included eggs. As there is no possible interaction between eggs and pupae, combinations involving both stages were not considered. Effective IGP was assessed when the prey was killed and consumed (Lucas, 2005). The natural mortality of each instar and adults was evaluated in Petri dishes containing only one individual of each species; dead individuals were subtracted from the observed mortality estimates in the IGP experiments.

2.2. Statistical analysis

IGP intensity was assessed as the proportion of replicates where IGP occurred. For each stage-specific combination, IGP rates on each involved species were compared by G-test. At species level, the symmetry index was calculated as follows: number of replicates in which a predator was preyed upon/ total number of replicates in which IGP occurred (Lucas et al., 1998; Lucas, 2005). This symmetry index was compared by G-test to a 50% theoretical index that corresponds to a symmetrical interaction (Scherrer, 1994).

In order to evaluate the vulnerability to IGP of the most exposed stages (eggs, 1st, and 2nd instars and pupae) of *H. axyridis*, comparisons were made with the respective stages of a second IGPrey species (*P. quatuordecimpunctata* or *C. maculata*) when facing a common IGPredator (*P. quatuordecimpunctata* or *C. maculata* different mobile stages). In the case of eggs, the mean number eaten was compared between IGPrey species. To do that, data normality and variance homogeneity were first evaluated by the Shapiro-Wilk and Levene's tests, respectively. As data followed a normal distribution, an ANOVA was performed to look for significant differences. In the case of the 1st and 2nd instars and pupae, their IGP intensities (proportion of replicates where those stages were preyed upon) were compared between IGPrey species. In this case, a binomial generalized linear model (GLM), where the presence/absence of IGP was represented with 1/0, respectively, was used to look for significant differences.

In order to evaluate the influence of age on the IGP intensity, stage-specific vulnerability indices were calculated as follows: number of replicates where IGP on stage X occurred/ total number of tests involving stage X. These results were compiled for each IGPredator species on the two other IGPrey species and compared using a binomial GLM with IGPrey species and IGPrey stage as fixed factors. For each IGPrey stage, pairwise comparisons between IGPrey species used the Tukey-Kramer test.

To assess the impact of the body weight difference between the IGPredator and IGPrey on the IGP intensity, body weight differences between IGPredator and IGPrey were calculated for each larval combination for the three species-species combinations and then correlated with IGP intensity according to Félix & Soares (2004). Logarithmic and linear functions were fitted to data sets and the best fit chosen.

All statistical analyses were performed using JMP PRO 15 software (SAS Institute, 2023).

3. RESULTS

Globally, 2025 IGP tests were carried out. For each species-species combination, 675 tests were performed, divided into 45 different stage-specific combinations each composed of 15 replicates (Table 1).

3.1. IGP at species level

3.1.1. IGP between *H. axyridis* and *C. maculata*

IGP between *H. axyridis* and *C. maculata* was observed in 57.8% of the tests that contained this pairing, considering all possible stage-combinations. The interaction was mutual, both species being IGPredator but also IGPrey. When IGP occurred, *H. axyridis* was the IGPredator in 64.1% of the tests, being significantly dominant in all combinations that involved earlier stages of *C. maculata* (except for adult-pupa and pupa combinations). *Harmonia axyridis* 4th and 3rd instars were also significantly dominant when paired with the respective same instars of *C. maculata*. As expected, eggs and 1st instar were the most vulnerable developmental stages of both species, being asymmetrically preyed on in most of the combinations (Table 1A). At species level, the interaction between these two predators was significantly asymmetrical in favour of the multi-coloured Asian ladybeetle ($G_1 = 18.49$, $P < 0.001$) (Fig. 1).

3.1.2. IGP between *H. axyridis* and *P. quatuordecimpunctata*

IGP between *H. axyridis* and *P. quatuordecimpunctata* was observed in 54.7% of the tests that contained this pairing, considering all possible stage-combinations. The interaction was mutual, both species being IGPredator and IGPrey. When IGP occurred, *H. axyridis* was the IGPredator in 75.3% of the tests, being significantly dominant in all combinations that involved the same or earlier stages of *P. quatuordecimpunctata* (except for adult-adult, 1st instar-1st instar, and pupa combinations). Eggs of both species and 1st instar of *P. quatuordecimpunctata* were the most vulnerable developmental stages, being asymmetrically preyed on in most of the combinations (Table 1B). At species level, the interaction between these two predators was significantly asymmetrical in favour of the multi-coloured Asian ladybeetle ($G_1 = 50.64$, $P < 0.001$) (Fig. 1).

Table 1. IGP intensity (proportion of IGP) and symmetry of interactions between the different instars of: A – *H. axyridis* (HA) - *C. maculata* (CM); B – *H. axyridis* (HA) - *P. quatuordecimpunctata* (P14); C – *P. quatuordecimpunctata* (P14) - *C. maculata* (CM). Ad – adult; Pp – pupa; L4 – 4th instar; L3 – 3rd instar; L2 – 2nd instar; L1 – 1st instar.

(A) *H. axyridis* vs *C. maculata*

Combination	*HA*	*CM*	df	G	*P*	
Ad-Ad	0	0	0,1	0	1	
Ad-Pp	0	6.67	1,3	1.72	0.19	
Ad-L4	0	46.67	1,15	6.9	0.009	**
Ad-L3	0	93.33	1,27	12.08	0.0005	***
Ad-L2	0	100	1,31	13.81	0.0002	***
Ad-L1	0	100	1,31	13.81	0.0002	***
Ad-Egg	0	100	1,31	13.81	0.0002	***
Pp-Ad	0	0	0,1	0	1	
Pp-L4	0	0	0,1	0	1	
Pp-L3	0	0	0,1	0	1	
Pp-L2	0	0	0,1	0	1	
Pp-L1	0	0	0,1	0	1	
L4-Ad	0	0	0,1	0	1	
L4-Pp	0	26.67	1,7	3.45	0.06	
L4-L4	0	60	1,19	8.63	0.003	**
L4-L3	0	93.33	1,27	12.08	0.0005	***
L4-L2	0	100	1,31	13.81	0.0002	***
L4-L1	0	100	1,31	13.81	0.0002	***
L4-Egg	0	100	1,31	13.81	0.0002	***
L3-Ad	20	0	1,7	3.45	0.06	
L3-Pp	0	0	0,1	0	1	
L3-L4	26.67	0	1,7	3.45	0.06	
L3-L3	0	86.67	1,27	12.08	0.0005	***
L3-L2	0	100	1,31	13.81	0.0002	***
L3-L1	0	100	1,31	13.81	0.0002	***
L3-Egg	0	100	1,31	13.81	0.0002	***
L2-Ad	53.33	0	1,15	6.9	0.0009	***
L2-Pp	0	0	0,1	0	1	
L2-L4	100	0	1,31	13.81	0.0002	***
L2-L3	20	0	1,7	3.45	0.06	
L2-L2	0	26.67	1,7	3.45	0.06	
L2-L1	0	100	1,31	13.81	0.0002	***
L2-Egg	0	100	1,31	13.81	0.0002	***
L1-Ad	73.33	0	1,23	10.34	0.0013	**
L1-Pp	0	0	0,1	0	1	
L1-L4	100	0	1,31	13.81	0.0002	***
L1-L3	80	0	1,23	10.36	0.0013	**
L1-L2	33.33	0	1,11	5.18	0.023	*
L1-L1	0	26.67	1,7	3.45	0.06	
L1-Egg	0	100	1,31	13.81	0.0002	***
Egg-Ad	100	0	1,31	13.81	0.0002	***
Egg-L4	100	0	1,31	13.81	0.0002	***
Egg-L3	100	0	1,31	13.81	0.0002	***
Egg-L2	100	0	1,31	13.81	0.0002	***
Egg-L1	26.67	0	1,7	3.45	0.06	

(B) *H. axyridis* vs *P. quatuordecimpunctata*

Combination	*HA*	*P14*	df	G	*P*	
Ad-Ad	0	0	0,1	0	1	
Ad-Pp	0	53.3	1,15	6.9	0.009	**
Ad-L4	0	93.3	1,27	12.08	0.0005	***
Ad-L3	0	100	1,27	12.08	0.0005	***
Ad-L2	0	100	1,31	13.81	0.0002	***
Ad-L1	0	100	1,31	13.81	0.0002	***
Ad-Egg	0	100	1,31	13.81	0.0002	***
Pp-Ad	0	0	0,1	0	1	
Pp-L4	0	0	0,1	0	1	
Pp-L3	0	0	0,1	0	1	
Pp-L2	0	0	0,1	0	1	
Pp-L1	0	0	0,1	0	1	
L4-Ad	0	0	0,1	0	1	
L4-Pp	0	33.3	1,11	5.18	0.02	*
L4-L4	0	86.7	1,27	12.08	0.0005	***
L4-L3	0	86.7	1,27	12.08	0.0005	***
L4-L2	0	93.3	1,27	12.08	0.0005	***
L4-L1	0	93.3	1,27	12.08	0.0005	***
L4-Egg	0	93.3	1,27	12.08	0.0005	***
L3-Ad	0	0	0,1	0	1	
L3-Pp	0	60	1,19	8.63	0.0033	**
L3-L4	0	0	0,1	0	1	
L3-L3	0	86.7	1,27	12.08	0.0005	***
L3-L2	0	100	1,31	13.81	0.0002	***
L3-L1	0	100	1,31	13.81	0.0002	***
L3-Egg	0	80	1,23	10.36	0.0013	**
L2-Ad	6.67	0	1,3	1.73	0.19	
L2-Pp	0	0	0,1	0	1	
L2-L4	33.33	0	1,11	5.18	0.02	*
L2-L3	0	0	0,1	1	1	
L2-L2	0	93.3	1,27	12.08	0.0005	***
L2-L1	0	100	1,31	13.81	0.0002	***
L2-Egg	0	100	1,23	10.36	0.0013	**
L1-Ad	6.67	0	1,3	1.73	0.19	
L1-Pp	0	0	0,1	1	1	
L1-L4	60	0	1,19	8.63	0.003	**
L1-L3	46.67	0	1,15	6.9	0.009	**
L1-L2	26.67	0	1,7	3.45	0.06	
L1-L1	0	0	0,1	1	1	
L1-Egg	0	100	1,31	13.81	0.0002	***
Egg-Ad	73.33	0	1,23	10.36	0.0013	**
Egg-L4	86.67	0	1,27	12.08	0.0005	***
Egg-L3	100	0	1,31	13.81	0.0002	***
Egg-L2	93.33	0	1,27	12.08	0.0005	***
Egg-L1	73.33	0	1,23	10.36	0.0013	**

(C) *C. maculata* vs *P. quatuordecimpunctata*

Combination	*CM*	*P14*	df	G	*P*	
Ad-Ad	0	0	0,1	0	1	
Ad-Pp	0	20	1,7	3.45	0.06	
Ad-L4	0	46.67	1,3	1.73	0.19	
Ad-L3	0	53.33	1,15	6.9	0.009	**
Ad-L2	0	100	1,31	13.81	0.0002	***
Ad-L1	0	100	1,31	13.81	0.0002	***
Ad-Egg	0	100	1,31	13.81	0.0002	***
Pp-Ad	0	0	0,1	0	1	
Pp-L4	6.67	0	1,3	1.73	0.19	
Pp-L3	0	0	0,1	0	1	
Pp-L2	0	0	0,1	0	1	
Pp-L1	0	0	0,1	0	1	
L4-Ad	13.33	0	1,3	1.73	0.19	
L4-Pp	0	73.33	1,23	10.36	0.0013	**
L4-L4	0	25	1,7	3.45	0.06	
L4-L3	0	73.33	1,23	10.36	0.0013	**
L4-L2	0	100	1,31	13.81	0.0002	***
L4-L1	0	100	1,31	13.81	0.0002	***
L4-Egg	0	100	1,31	13.81	0.0002	***
L3-Ad	40	0	1,11	5.18	0.02	*
L3-Pp	0	66.67	1,19	8.63	0.0033	**
L3-L4	26.67	0	1,7	3.45	0.06	
L3-L3	0	13.33	1,3	1.73	0.19	
L3-L2	0	80	1,23	10.36	0.0013	**
L3-L1	0	100	1,31	13.81	0.0002	***
L3-Egg	0	100	1,31	13.81	0.0002	***
L2-Ad	53.33	0	1,15	6.9	0.009	**
L2-Pp	0	6.67	1,3	1.73	0.19	
L2-L4	80	0	1,23	10.36	0.0013	**
L2-L3	0	0	0,1	0	1	
L2-L2	0	26.67	1,7	3.45	0.06	
L2-L1	0	66.67	1,19	8.63	0.0033	**
L2-Egg	0	100	1,31	13.81	0.0002	***
L1-Ad	100	0	1,31	13.81	0.0002	***
L1-Pp	0	0	0,1	0	1	
L1-L4	100	0	1,31	13.81	0.0002	***
L1-L3	80	0	1,23	10.36	0.0013	**
L1-L2	80	0	1,23	10.36	0.0013	**
L1-L1	6.67	20	1,11	0.34	0.56	
L1-Egg	0	100	1,31	13.81	0.0002	***
Egg-Ad	100	0	1,31	13.81	0.0002	***
Egg-L4	100	0	1,31	13.81	0.0002	***
Egg-L3	100	0	1,31	13.81	0.0002	***
Egg-L2	100	0	1,31	13.81	0.0002	***
Egg-L1	100	0	1,31	13.81	0.0002	***

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; asterisks indicate differences in symmetry of interactions against a 50% theoretical interactions between protagonists.

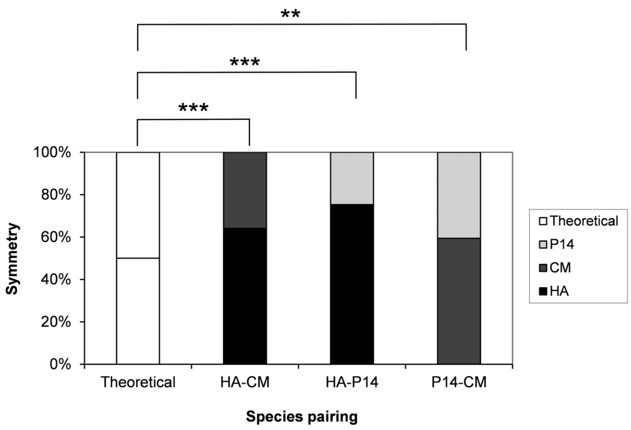

Fig. 1. Specific symmetry (at the species level) in intraguild confrontations between pairs of coccinellid species: *H. axyridis* (HA) - *C. maculata* (CM); *H. axyridis* (HA) - *P. quatuordecimpunctata* (P14); *P. quatuordecimpunctata* (P14) - *C. maculata* (CM). **P* < 0.05; ***P* < 0.01; ****P* < 0.001. An asterisk indicates an asymmetrical interaction between species.

3.1.3. IGP between *C. maculata* and *P. quatuordecimpunctata*

IGP between *C. maculata* and *P. quatuordecimpunctata* was observed in 59.1% of the tests that contained this pairing, considering all possible stage-combinations. The interaction was mutual, both species being IGPredator and IGPrey. When IGP occurred, *C. maculata* was the IGPredator in 59.1% of the tests, being significantly dominant in all combinations that involved earlier stages of *P. quatuordecimpunctata* (except for adult-pupa, adult-4th instar, and pupa combinations). As expected, eggs and 1st instar were the most vulnerable developmental stages of both species, being asymmetrically preyed upon in most of the combinations (Table 1C). At the species level, the interaction between *C. maculata* and *P. quatuordecimpunctata* was significantly asymmetrical in favour of the former (G1 = 7.26, P = 0.007) (Fig. 1).

3.2. Comparative vulnerability of early instars and immobile stages

Overall, eggs of *P. quatuordecimpunctata* were more vulnerable to *C. maculata* than eggs of *H. axyridis* ($F_{1,148}$ = 15.63; *P* < 0.001). Similarly, IGP by *P. quatuordecimpunctata* on *C. maculata* eggs was higher than on *H. axyridis* eggs ($F_{1,148}$ = 13.79; *P* < 0.001). Vulnerability of eggs of *H. axyridis* to *C. maculata* or *P. quatuordecimpunctata* was, however, different between IGPredator developmental stages (Fig. 2A). More *P. quatuordecimpunctata* eggs were consumed by 1st ($F_{1,28}$ = 93.39; *P* < 0.0001), 2nd ($F_{1,28}$ = 21.66; *P* < 0.0001) and 3rd ($F_{1,28}$ = 9.32; *P* = 0.005) instars of *C. maculata* when compared to eggs of *H. axyridis*. More *C. maculata* eggs were consumed by 1st instars ($F_{1,28}$ = 4.87; *P* = 0.04) and adults ($F_{1,28}$ = 21.65; *P* < 0.0001) of *P. quatuordecimpunctata* when compared to eggs of *H. axyridis*.

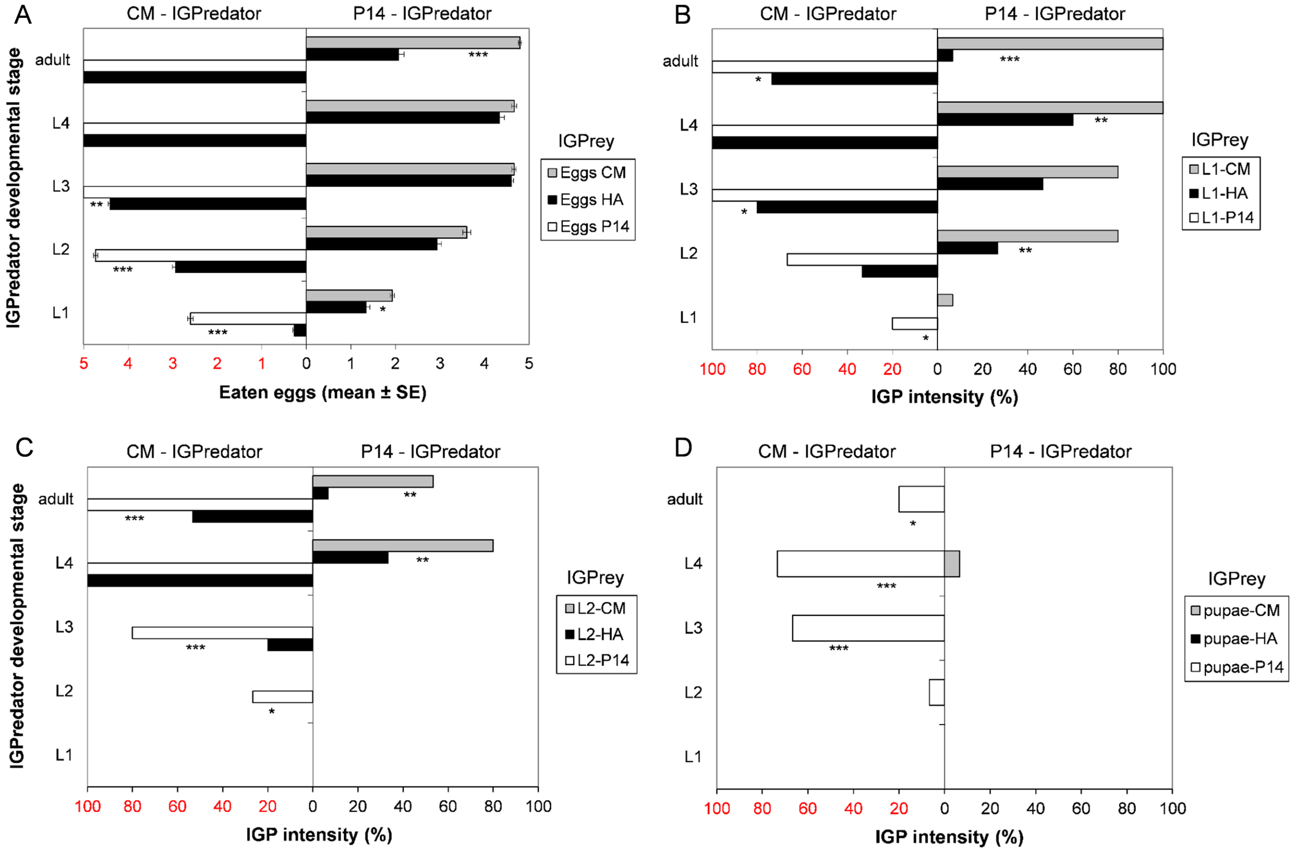

Fig. 2. Comparative vulnerability of *H. axyridis* (HA) (A) eggs, (B) 1st instar (C) 2nd instar, or (D) pupae with that of the same stage of a second coccinellid species (*P. quatuordecimpunctata* (P14) or *C. maculata* (CM)) when facing the 3rd coccinellid species as a potential IGPredator. **P* < 0.05; ***P* < 0.01; ****P* < 0.001; asterisks indicate differences between IGPrey species within stages.

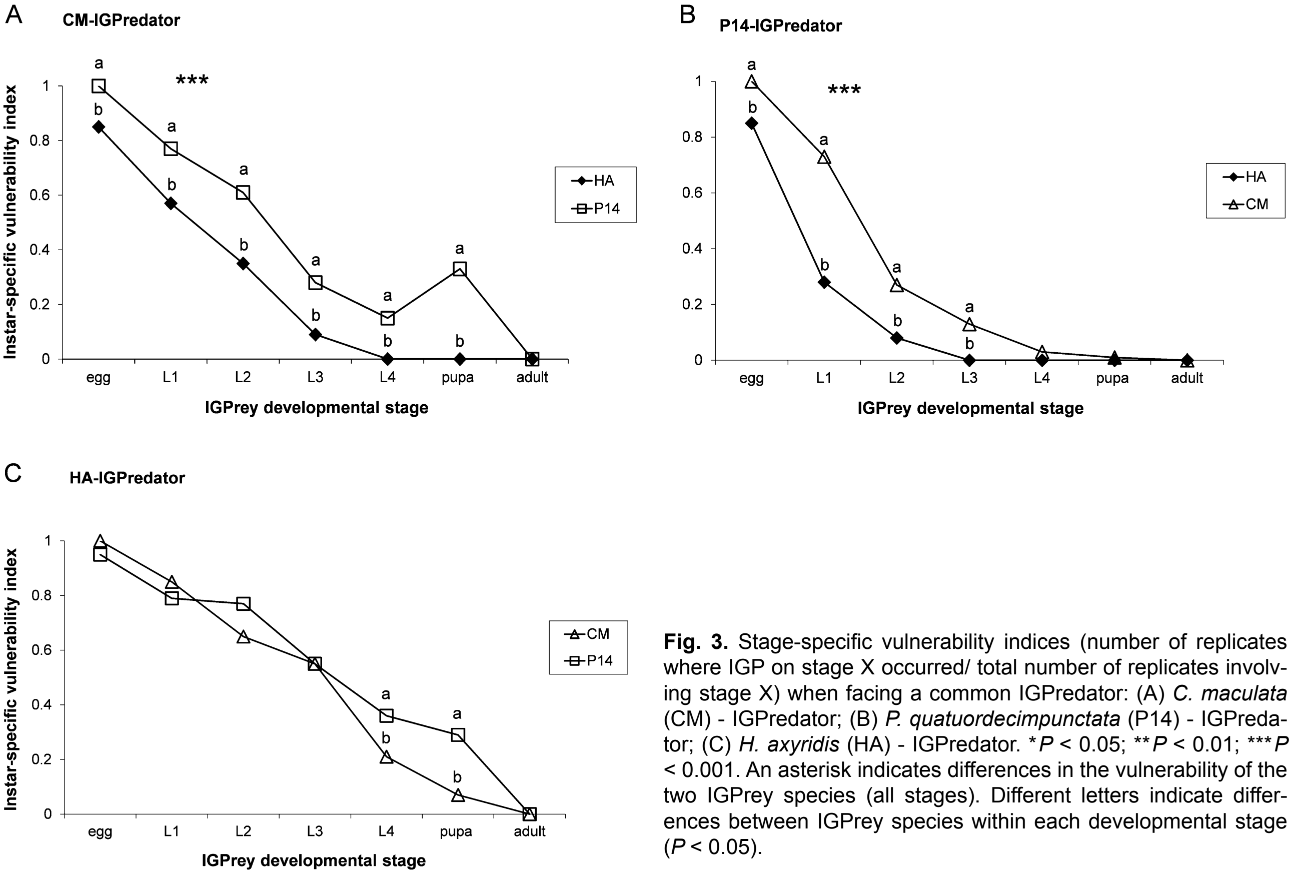

Fig. 3. Stage-specific vulnerability indices (number of replicates where IGP on stage X occurred/ total number of replicates involving stage X) when facing a common IGPredator: (A) *C. maculata* (CM) - IGPredator; (B) *P. quatuordecimpunctata* (P14) - IGPredator; (C) *H. axyridis* (HA) - IGPredator. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$. An asterisk indicates differences in the vulnerability of the two IGPrey species (all stages). Different letters indicate differences between IGPrey species within each developmental stage ($P < 0.05$).

Overall, 1st instars of *P. quatuordecimpunctata* were more vulnerable to *C. maculata* than 1st instars of *H. axyridis* ($Chi_{1,144} = 14.90$; $P < 0.001$). Similarly, IGP by *P. quatuordecimpunctata* on *C. maculata* 1st instars was higher than on *H. axyridis* 1st instars ($Chi_{1,144} = 46.34$; $P < 0.001$). Vulnerability of the 1st instars of *H. axyridis* to *C. maculata* or *P. quatuordecimpunctata* was, however, different between IGPredator developmental stages (Fig. 2B). More *P. quatuordecimpunctata* 1st instars were consumed by 1st ($Chi_{1,28} = 4.49$; $P = 0.034$) and 3rd ($Chi_{1,28} = 4.49$; $P = 0.034$) instars and adults ($Chi_{1,28} = 6.16$; $P = 0.013$) of *C. maculata* when compared to 1st instars of *H. axyridis*. More *C. maculata* 1st instars were consumed by 2nd ($Chi_{1,28} = 9.05$; $P = 0.003$) and 4th ($Chi_{1,28} = 9.83$; $P = 0.002$) instars and adults ($Chi_{1,28} = 34.11$; $P < 0.001$) of *P. quatuordecimpunctata* than 1st instars of *H. axyridis*.

Overall, 2nd instars of *P. quatuordecimpunctata* were more vulnerable to *C. maculata* than 2nd instars of *H. axyridis* ($Chi_{1,144} = 27.99$; $P < 0.001$). Similarly, IGP by *P. quatuordecimpunctata* on *C. maculata* 2nd instars was higher than on *H. axyridis* 2nd instars ($Chi_{1,144} = 15.28$; $P < 0.001$). Vulnerability of the 2nd instars of *H. axyridis* to *C. maculata* or *P. quatuordecimpunctata* was, however, different between IGPredator developmental stages (Fig. 2C). More *P. quatuordecimpunctata* 2nd instars were consumed by 2nd ($Chi_{1,28} = 6.16$; $P = 0.013$) and 3rd ($Chi_{1,28} = 11.56$; $P < 0.001$) instars and adults ($Chi_{1,28} = 11.87$; $P < 0.001$) of *C. maculata* when compared to 2nd instars of *H. axyridis*. More *C. maculata* 2nd instars were consumed by 4th instars ($Chi_{1,28} = 6.95$; $P = 0.008$) and adults ($Chi_{1,28} = 8.58$; $P = 0.003$) of *P. quatuordecimpunctata* when compared to 2nd instars of *H. axyridis*.

No pupae of *H. axyridis* were consumed, either by *C. maculata* or *P. quatuordecimpunctata*, while these ones were consumed by *H. axyridis* or the other predator. Overall, pupae of *P. quatuordecimpunctata* were more vulnerable to *C. maculata* than pupae of *H. axyridis* ($Chi_{1,144} = 47.04$; $P < 0.001$). IGP on pupae of *C. maculata* by *P. quatuordecimpunctata* was not different than on *H. axyridis* pupae ($P > 0.05$). Vulnerability of pupae of *P. quatuordecimpunctata* was, however, different between IGPredator developmental stages (Fig. 2D). More *P. quatuordecimpunctata* pupae were consumed by 3rd ($Chi_{1,28} = 19.09$; $P < 0.001$) and 4th ($Chi_{1,28} = 22.03$; $P < 0.001$) instars and adults ($Chi_{1,28} = 4.49$; $P = 0.034$) of *C. maculata* when compared to pupae of *H. axyridis*.

3.3. Stage-specific vulnerability of the three species

Vulnerability to IGP decreased with age for the three ladybeetle species ($P < 0.001$) (Figs 3A, B, C). Overall, *H. axyridis* was less vulnerable than *P. quatuordecimpunctata* ($Chi_{1,1048} = 38.50$; $P < 0.001$) or *C. maculata* ($Chi_{1,1048} = 27.21$; $P < 0.001$) when facing the same IGPredator (Figs 3A, B). When *C. maculata* was the IGPredator, the different developmental stages of *H. axyridis*, except adults, showed a significantly lower vulnerability than the respective stages of *P. quatuordecimpunctata* (Tukey-Kramer test $P < 0.05$) (Fig. 3A). When *P. quatuordecimpunctata* was the IGPredator, vulnerability indices of eggs, 1st, 2nd, and 3rd instars of *H. axyridis* were also significantly lower than

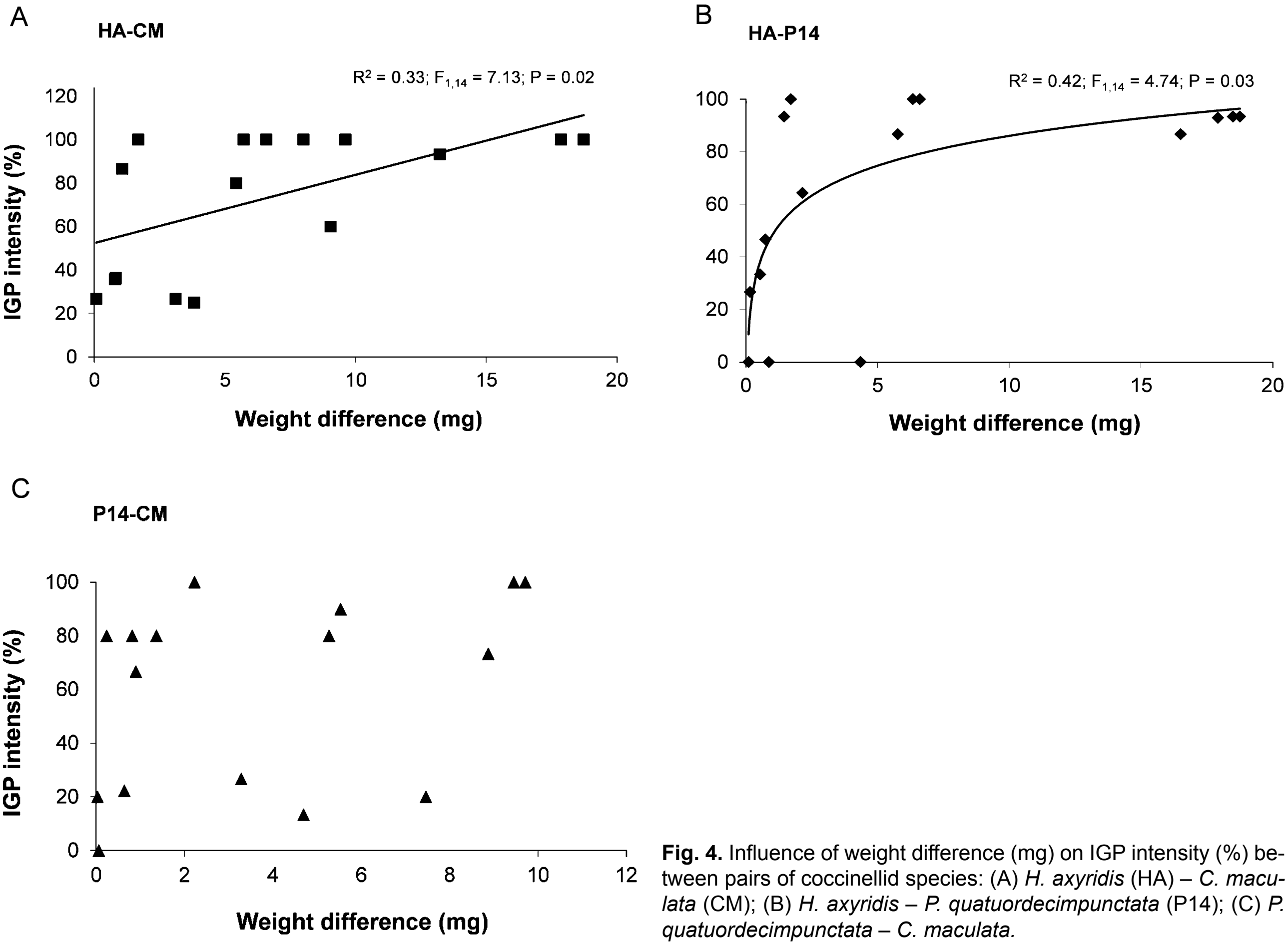

Fig. 4. Influence of weight difference (mg) on IGP intensity (%) between pairs of coccinellid species: (A) *H. axyridis* (HA) – *C. maculata* (CM); (B) *H. axyridis – P. quatuordecimpunctata* (P14); (C) *P. quatuordecimpunctata – C. maculata.*

those of *C. maculata* (Fig. 3B). When *H. axyridis* was the IGPredator, both *C. maculata* and *P. quatuordecimpunctata* were, overall, equally vulnerable ($\mathrm{Chi}_{1,1048} = 2.99$; $P = 0.084$). Only 4th instars and pupae of *P. quatuordecimpunctata* were preyed on more often than those of *C. maculata* (Tukey-Kramer test $P < 0.05$) (Fig. 3C). *Harmonia axyridis* eggs were never preyed on at 100% when compared to *C. maculata* or *P. quatuordecimpunctata*, and no 4thinstars or pupae were ever preyed upon by these two species.

3.4. Correlation between weight difference and IGP intensity

Weight differences between IGPredator and IGPrey instars were calculated and plotted with respective IGP intensity (Figs 4A, B, C). Significant relationships were observed between IGP intensity and weight difference in the combination *H. axyridis-C. maculata* ($R^2 = 0.33$; $F_{1,14} = 7.13$; $P = 0.02$) (Fig. 4A) and in the combination *H. axyridis-P. quatuordecimpunctata* ($R^2 = 0.42$; $F_{1,14} = 4.74$; $P = 0.03$) (Fig. 4B). No significant relation was found in the combination *P. quatuordecimpunctata-C. maculata* (Fig. 4C).

4. DISCUSSION

This study demonstrated that, while *H. axyridis* is a dominant IGPredator, it was highly susceptible to IGP by both competitor species mostly during egg and 1st instar stages. Considering the susceptibility of the different stages, all those of *H. axyridis* were less vulnerable than those of *P. quatuordecimpunctata* or *C. maculata* when facing the same potential IGPredator. As hypothesized, vulnerability to IGP decreases with the age of larvae for the three species. Size difference of protagonists was also important in confrontations.

This study, with all stages taken into account, clearly proved that *H. axyridis* was the most efficient IGPredator, performing asymmetrical interactions in 64% of the cases with the native *C. maculata* and 75% of the cases with the invasive *P. quatuordecimpunctata*. However, contrary to some other studies, we showed that *H. axyridis* was vulnerable to IGP since eggs, 1st and 2nd instars were consumed by the two other ladybird species. Cottrell (2007) noted that *C. maculata* larvae often accepted *H. axyridis* eggs in first contact even if they are not suitable for the development of its 1st or 3rd instars (Cottrell, 2004). Our results contrast with experiments of Ware & Majerus (2008) in Great Britain, where no *H. axyridis* 1st instars were consumed by *P. quatuordecimpunctata*. However, we observed a lower vulnerability of the eggs and less mobile instars of *H. axyridis* compared to the other species. In presence of *C. maculata* as an IGPredator, eggs, 1st and 2nd instars of *P. quatuordecimpunctata* were preyed on more often than those of *H. axyridis*. The same relationships were observed when *P. quatuordecimpunctata* was the IGPredator and *C. maculata* and *H. axyridis* the IGPrey. Thus, even if *H. axyridis* was preyed upon by other ladybeetles, some chemical or behavioural protection seems effective in reducing predation over its developmental stages (Sato & Dixon, 2004; Pell et al., 2008; Sloggett et al., 2011).

A significant decrease in IGP with increased age of juveniles was observed for the three species. In *H. axyridis*, later instars were better protected from predation. No 4th instars were preyed by *C. maculata*, and no 3rd and 4th instars by *P. quatuordecimpunctata*. Experiments by Yasuda et al. (2001) demonstrated that 3rd and 4th instars were more aggressive than earlier ones, which could explain the reduced IGP rate on these instars. Spines are also well developed in the 3rd and 4thinstars of *H. axyridis*, but not in earlier ones (Koch, 2003). Ware & Majerus (2008) implicated the role of spines as superior physical defences in the larval stages of *H. axyridis* compared to other species. The absence of efficient spines could explain high rates of IGP on *H. axyridis* early instars. Later instars seem thus less vulnerable to predation, which would give a great advantage in the field, and could explain in part its invasive success.

The other vulnerable stage to IGP in coccinellids is the pupa, as it is immobile over a long time, with few defensive mechanisms other than flicking up and down (combined with gin traps) or chemical defence (Lucas et al., 1998, 2000). For example, *C. maculata* pupates outside the plant, far from aphid colonies, to avoid predation in this vulnerable stage (Lucas et al., 2000; Labrie et al., unpubl. data). In our experiment, the pupae of *C. maculata* and *P. quatuordecimpunctata* were preyed upon by *H. axyridis*. In contrast, *H. axyridis* pupae were never preyed upon by *P. quatuordecimpunctata* nor *C. maculata*. Similarly, the study by Félix & Soares (2004) demonstrated that *H. axyridis* pupae were almost invulnerable to IGP by *C. undecimpunctata*. Size, the strength of the integument, and distastefulness (Félix & Soares, 2004), as well as defensive behaviour such as flicking up and down, may explain the lower vulnerability of the pupal stage of this species. Other studies demonstrated such invulnerability for chrysopids and syrphids pupae to IGP by coccinellids and mirids (Fréchette et al., 2007; Ingels & De Clercq, 2011; Nedvěd et al., 2013). The pupal stage could be less vulnerable to predation than previously thought (Lucas, 2005). However, Fremlin (2007) observed *Chrysoperla carnea* (Stephens) attacking *H. axyridis* pupae. Furthermore, Labrie et al. (2006) demonstrated that *H. axyridis* pupae take more time to develop into adults than *C. maculata*, potentially increasing its vulnerability to predation. More studies are needed to clearly establish the range of potential IGPredators of *H. axyridis* pupae.

Many studies refer to the importance of body size in IGP, where in most cases, the difference in size determines the outcome of the interaction, in which smaller individuals are killed by larger ones (Polis et al., 1989; Snyder et al., 2004; Lucas, 2012). Thus, as differences between IGPredator and IGPrey increase, IGP intensity rises (Majerus, 1994). In this study, this relationship was significant in the two combinations involving *H. axyridis* larvae, but not for the interaction between *P. quatuordecimpunctata* and *C. maculata*. Félix & Soares (2004) demonstrated an increase in IGP intensity by *H. axyridis* on *C. undecimpunctata* with an increase in body weight difference between protagonists. Ware & Majerus (2008) demonstrated that the level of IGP was directly correlated to differences in size between 4th instars of *H. axyridis* and *H. quadripunctata* (Pontoppodan) or *Anatis ocellata* (Linnaeus). Larvae of the largest species, *A. ocellata*, won the majority of encounters with *H. axyridis*, while the smallest species, *H. quadripunctata*, lost most of the encounters. Our experiment also demonstrated that *H. axyridis* has to be larger than competitors to succeed in its interactions with other ladybeetles, which strongly suggests that this species is not free from significant predation pressure in the field. Such a relationship was not observed between *C. maculata* and *P. quatuordecimpunctata*, even if this ladybeetle is the smallest of the three protagonists. Relative IGP advantages among these two coccinellids may be determined by behavioural and defensive differences not related to size (Snyder et al., 2004). More studies have to be performed with this small invasive species.

In the field, there are key factors influencing the outcome of IGP among coccinellids exploiting a shared resource (Lucas, 2005, 2012). For example, the time of colonisation, voltinism, and developmental time will determine the species' relative body size at a specific time and thus, their IGPrey/IGPredator status. The time of emergence from overwintering sites should influence the time of colonisation of fields. *Harmonia axyridis* overwinters inside houses, which provides a cold-free and potentially enemy-free space (Labrie et al., 2008; but see Nalepa & Weir, 2007). This may explain why, some years, *H. axyridis* returns to fields in spring earlier than other species (E. Lucas, pers. commun.), which could lead to higher IGP opportunities. This could account for the displacement of some coccinellid species observed in orchards since the establishment of *H. axyridis* (Brown & Miller, 1998; Brown, 2003). During summer, the time of colonisation of coccinellid species could be also crucial for the outcome of IGP. Jansen & Hautier (2008) demonstrated that *H. axyridis* arrived 7 to 8 days later than *P. quatuordecimpunctata* and *C. septempunctata* in potato fields. Other studies demonstrated that *C. maculata* colonized wheat or corn earlier than *H. axyridis* (Musser & Shelton, 2003; Nault & Kennedy, 2003; Labrie, unpubl. data). Our experiment with *P. quatuordecimpunctata*, a much smaller ladybeetle than *H. axyridis*, in which later instars and adults preyed upon eggs or earlier instars of *H. axyridis*, demonstrated that body size difference between individual protagonists at the time of the encounter rather than body size difference between species is the main factor determining the outcome of the interaction. IGP by *C. maculata* later instars and adults on eggs and early instars of *H. axyridis* was also important so this species might not be free from predation pressure in the fields. However, differences in within-plant distribution on corn plants can be found between *C. maculata* and *H. axyridis*, the indigenous occupying lower parts of the corn than *H. axyridis* (Musser & Shelton, 2003; Hoogendoorn

& Heimpel, 2004;), thus reducing potential interactions between species.

Developmental time could also be important to determine the outcome of IGP. *Harmonia axyridis* developmental time is similar to *C. maculata,* however, it develops more rapidly than *C. maculata* in 2nd instars (Labrie et al., 2006), which are more vulnerable to predation. This developmental pattern could be crucial in the fields if both species are present at the same time, allowing *H. axyridis* to avoid IGP or to be the IGPredator in such encounters.

Many other factors have to be taken into account when evaluating the risk of IGP between coccinellid species. One obvious limitation of this study is that interactions were confined to Petri-dish arenas. In natural conditions, escape behaviour and the presence of different food sources and refuges may greatly reduce the risk of IGP. Furthermore, intraspecific competition, such as cannibalism, can affect IGP intensity and impact on competing species. In natural populations of *H. axyridis*, cannibalism occurred in more than 90% of all clusters (Osawa, 1989), and approximately 30% of eggs were killed by sibling cannibalism (Osawa, 1993). It has been also demonstrated that this species can develop only on eggs of its own species (Cottrell, 2005, 2007).

In our study, *H. axyridis* eggs, 1st and 2nd instars were vulnerable to predation by two co-occurring ladybird species. More studies are needed in the field to analyse the temporal dynamics of *H. axyridis* in regard to the other guild members in order to establish the real impact of IGP by or on the Asiatic ladybird.

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