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Can developmental and behavioral characteristics of the multicolored Asian lady beetle *Harmonia axyridis* explain its invasive success?

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Abstract

Major impacts of biological invasions are widely recognized and underscore the need to understand the relation between life-history traits of invasive species and the invasion process. Growth of juveniles and adult survival of invasive species are key factors in invasion process. Life-history traits that increase juvenile fitness including increased rates of development and behavioral characteristics that facilitate competitive success such as increased predator efficiency and foraging ability may explain invasiveness of a species. Invasion of *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) in North America provides an opportunity to investigate life-history traits of juveniles of an invasive species. Here, we evaluate both developmental and behavioral traits that may explain the success of *H. axyridis* by comparing it to an ecologically similar indigenous species *Coleomegilla maculata lengi* Timberlake (Coleoptera: Coccinellidae). Three points may contribute to the invasiveness of *H. axyridis*. First, development of *H. axyridis* was faster during the 2nd larval instar than *C. maculata*, a characteristic that may reduce vulnerability at young instars. Second, *H. axyridis* reached the 4th instar more rapidly than *C. maculata*. The 4th instar of *H. axyridis* was also characterized by higher predation efficiency with increased voracity, lethal contact and search efficiency of pea aphids *Acyrthosiphon pisum*. Finally, surprisingly, a 5th larval instar occured in 33% of the individuals of *H. axyridis* and was characterized by the same developmental time, but with increased voracity and weight gain compared to 4th larval instars, suggesting an increased fitness of these individuals. These developmental characteristics coupled with increased predation efficiency and behavioral characteristics enhanced the juvenile growth and predatory abilities of this species and may contribute to the invasive ability of *H. axyridis*.

Introduction

Biological invasions are having major ecosystem impacts and are thought to be the second leading cause of biodiversity loss (Pimentel et al. 2000; Vitousek et al. 1996). The need to limit the impact of nonindigenous species on natural communities has generated many recent experimental studies (Kolar and Lodge 2001; Keane and Crawley 2002; Snyder et al. 2004). Many biological and environmental factors could contribute to the invasiveness of species (Marco et al. 2002). It is thought that life-history traits like increased developmental rate, fecundity and fertility are important for successful invasion and establishment (Sakai et al. 2001; Shea and Chesson 2002; Marco et al. 2002; Lanzoni et al. 2004) and their knowledge are of basic importance to develop a better understanding of interspecific interactions among exotic and native species (Krijger et al. 2001; Lanzoni et al. 2004). The key factor in invasion process is juvenile growth, as safe growth in these vulnerable stages can ensure high population growth in the new environment (Marco et al. 2002). Release from natural enemies and parasites (Kimberling 2004; Hierro et al. 2005), resources productivity of the new environment (Marco et al. 2002) and increased opportunities for colonization caused by anthropogenic disturbances (Mack et al. 2000) can also increase the invasibility of a species. Ecologists are limited in their ability to identify likely successful invaders prior to establishment (Snyder et al. 2004). Hence, there is a need to understand the underlying biological mechanisms explaining invader success (Keane and Crawley 2002; Shea and Chesson 2002; Kimberling 2004).

The multicolored Asian lady beetle, *Harmonia axyridis* Pallas, has been released many times in North America since 1916 as a classical biological control agent against aphids (Gordon 1985). The first established population was reported in Louisiana in 1988 (Chapin and Brou 1991) and it spread rapidly across North America the following years (Tedders and Schaefer 1994; Colunga-Garcia and Gage 1998). This coccinellid appeared in Canada in 1994 (Coderre et al. 1995) and is now widely present in many ecosystems (Lucas et al. 2002; Lucas et al. in preparation; Turnock et al. 2003). This species is polyphagous and eurytopic (Iablokoff-Khnzorian 1982; Tedders and Schaefer 1994; Hodek and Honek 1996; Lucas et al. 1997a; Koch 2003). *Harmonia axyridis* is a strong intraguild predator of the other coccinellid species (Cottrell and Yeargan 1998; Yasuda and Ohnuma 1999; Yasuda et al. 2001; Burgio et al. 2002; Cottrell 2004; Félix and Soares 2004; Snyder et al. 2004), possibly of chrysopids (Brown 2003), and some studies supposed that it is displacing competitively *Coccinella septempunctata* L. in mid-Western USA (Brown and Miller 1998; Reitz and Trumble 2002; Brown 2003), *Coccinella transversoguttata* Brown in Maine (USA) (Alyokhin and Sewell 2004) and *Cycloneda sanguinea* (L.) in Florida (USA) (Michaud 2002). Intraguild predation (IGP) has been reported between *H. axyridis* and the native *Coleomegilla maculata lengi* Timberlake in laboratory and in field, with asymmetric interaction in favor of *H. axyridis* (Cottrell and Yeargan 1998; Cottrell 2004); greater impact of the exotic species can be expected in the field on native species (Yasuda et al. 2001; Cottrell 2004).

Harmonia axyridis dominate aphidophagous guilds in some agricultural ecosystems in part due to high fecundity (Iablokoff-Khnzorian 1982), large body size (Michaud 2002), polyphagous feeding (Koch 2003), aggressive behavior (Cottrell and Yeargan 1998; Yasuda and Ohnuma 1999; Yasuda et al. 2001; Cottrell 2004; Félix and Soares 2004; Snyder et al. 2004), high mobility (Osawa 2000; With et al. 2002) and low susceptibility to pathogens (Hoogendoorn and Heimpel 2002; Cottrell and Shapiro-Ilan 2003; Firlej et al. 2005;). Rapid juvenile development of *H. axyridis* relative to indigenous species could be another characteristic of invasiveness of this species (Lanzoni et al. 2004).

Another attribute that may determine predator success in agricultural ecosystems is their searching strategies (Lanzoni et al. 2004; Munyaneza and Obrycki 1998b; Osawa 2000). The searching strategies resulting in the most successful prey capture can favor individuals in a species, determine the functional response and influence the numerical and developmental responses of a species (Munyaneza and Obrycki 1998a; Dixon 2000). In this regard, it is supposed that an invasive species will have better searching strategies that result in higher predation efficiency than indigenous ones (Kimberling 2004).

The objective of this study was to evaluate some developmental and behavioral characteristics that could explain this invasion success in Canadian ecosystems. We chose to compare the invasive species *H. axyridis* with the native *C. maculata* because they share many similar characteristics: they belong to the same tribe Coccinellini (Iablokoff-Khnzorian 1982), they are polyphagous (Hodek and Honek 1996), they overlap spatially and temporally in some crops (sweet corn: Musser and Shelton 2003; corn: Hoogendoorn and Heimpel 2004; Labrie et al. in preparation), and the comparison with an indigenous species can allow us to point out which juvenile characteristics may explain invasiveness of *H. axyridis.* We hypothesized that (1) the preimaginal developmental time of *H. axyridis* will be shorter than *C. maculata* and (2) the predation efficiency will be greater for *H. axyridis* than *C. maculata*.

Material and methods

Insects

Harmonia axyridis were collected in agricultural fields around Montreal, Quebec (74°00′ W, 45°21′ N) in June 2003. *Coleomegilla maculata* were collected at overwintering sites near St-Hyacinthe, Quebec (72°56′ W, 45°39′ N) in April 2003. Adults were maintained in the laboratory in muslin cages at constant temperature (24 °C) photoperiod (16L : 8D) and relative humidity (RH : 60–75%). Both species were fed a mixed diet of pea aphids, *Acyrthosiphon pisum* Harris, a liver based artificial diet (Firlej et al. in preparation) and eggs of *Ephestia kuehniella* Zeller (Lepidoptera : Pyralidae). The pea aphid *A. pisum* used in development experiment were maintained on broadbean plants *Vicia faba* L. under the same conditions.

Preimaginal development

Eggs of each coccinellid species were removed from cages and maintained in control chambers between 23 and 25 °C, 16L:8D, 60–75% RH until eclosion. One 1st instar larvae of each species was placed individually on one broadbean plant encaged in a transparent plastic container of 30 cm height and 10 cm width with muslin openings. This set-up was repeated 15 times for each species. All cages were maintained under identical conditions. The number of *A. pisum* offered to predator larvae depended on the developmental stage of coccinellid (Soares et al. 2001). Based on preliminary tests we offered to coccinellid larvae: 10 individual aphids for 1st instar, 20 for 2nd, 30 for 3rd, 40 for 4th, 60 for 5th (when present). Aphids were deposited daily on each plant. Gravid female aphids were not used because of their capacity to reproduce and increase aphid density. Aphids of 2nd or 3rd instar were added daily in order to keep the density constant. Aphids were weighed to assess biomass availability for coccinellids. Coccinellid larvae were weighed each day before adding new aphids. The presence of exuviae was noted and examined to determine the larval instar. Pre-imaginal developmental time was calculated in days from the date of hatching to adult emergence. Developmental time was also recorded for each predator larvae instar separately. Survival was determined as the proportion of larvae that emerged successfully as adults. Adult emergence (AE) and growth index (GI) were calculated (Table 1).

Survival, growth index and adult emergence of both species were compared with χ^2-test. We compared developmental time between species for each larval instar using ANOVA. Squared root transformations were used on developmental time to normalize data distribution (Sokal and Rohlf 1995). All statistical analyses were performed with JMP 5.0® (SAS Institute).

Predation efficiency

The number of aphids eaten/day by each coccinellid was counted and the voracity (V) was determined (Lucas et al. 1998) (Table 1). No correction of the voracity were made with a control consisting of a plant without predators because mortality of aphids was easily determined as consumed by coccinellids or desiccated at the bottom of the plant. Partially consumed aphids were not used to calculate voracity. Relative weight gain for total preimaginal development and the preimaginal relative growth rate (RGR) for each larval instar were calculated (Table 1). Weights of aphids and predator larvae permitted calculation of conversion efficiency (CE) that evaluated the efficiency of food assimilation of each species (Table 1).

Voracity, relative weight gain, RGR and CE were compared between larval instars of the two species with ANOVAs (Sokal and Rohlf 1995). Squared root transformation was used on voracity and CE to normalize data distribution (Sokal and Rohlf 1995).

Foraging behavior

Foraging behavior of each individual of the two species was observed 24 h after each molt. Observations were done over 20 min with the Software Observer 2.0 (Noldus Information Technology b.v. 1989, 1990) and the frequency and duration of the following behaviors were noted:

- *Resting*: Predators remain stationary, but not feeding.

Table 1. Formulae of the different developmental and behavioral characteristics measured.

Measures	Unity	Formulae	References
Preimaginal development			
Total survival	%	Percentage of larvae emerging as adults	
Adult emergence	%	$\frac{\text{Number of adults emerged}}{\text{Number of pupae}} \times 100$	Omkar and Srivastava (2003)
Growth index (GI)	%/days	$\frac{\text{\% Pupation}}{\text{Developmental time}}$	Omkar and Srivastava (2003)
Predation efficiency			
Voracity (V)	N aphids/day	Number of aphids eaten by day	Lucas et al. (1998)
Relative weight gain	mg	$\frac{\text{Larval weight}_T\text{(mg)}-\text{Larval weight}_{T-1}\text{(mg)}}{\text{Larval weight}_T\text{(mg)}}$	
Relative growth rate (RGR)	mg/days	$\frac{\text{Initial adult weight (mg)}-\text{Initial L4weight (mg)}}{\text{Developmental time}}$	Omkar and Srivastava (2003)
Conversion efficiency (CE)	%	$\frac{\text{Weight of predator during development (mg)}}{\text{Weight of ingested biomass (mg)}}$	Schanderl (1987)
Lethal contact (LC)	%	$\frac{\text{Number of contacts resulting in the death of aphids}}{\text{Total number of aphids contacted}}$	Lucas et al. (1997)
Search efficiency (SE)	%	$\frac{\text{Total number of aphids contacted}}{\text{Total number of aphids on the plant}}$	

T: time at end of larval stage; *T*−1: time at beginning of larval stage.

- *Extensive searching*: Predators walk in fast linear movements between prey patches (Dixon 1959; Ettifouri and Ferran 1993). Predators shift from extensive search into handling mode upon encountering a prey (Rosenheim and Corbett 2003).
- *Intensive searching*: Predators walk in slow and sinuous movements (Ettifouri and Ferran 1993). This represents the local search that foraging predators often express once within a patch of prey (Rosenheim and Corbett 2003).
- *Handling*: Predators handle (e.g. ingesting or digesting) a prey item. Predators remain stationary and do not consume other prey within the area of discovery. Predators shifts from handling into intensive searching mode upon completion of handling time. (Rosenheim and Corbett 2003).
- *Attacking*: Predator attacks an aphid, and the number of successful attacks is counted. We also counted the total number of contacts with aphids, which allowed calculation of lethal contact (LC) and the search efficiency (SE) index (Table 1).
- *Grooming*: Predators clean palps on the ground or clean legs with movement of mandibles.

Statistical analyses were performed with MANOVA for overall differences between species and stages (Minoretti and Weisser 2000; McPeek 2004). Duration and frequency of intensive and extensive searching, resting, handling and grooming time were all included as dependent variables in the overall multivariate test. Squared-root data were used on dependent variables for statistical analyses to normalize data distribution. If *H. axyridis* was identified as differing significantly from *C. maculata* in the multivariate analysis, the same model was applied to each behavioral variable separately in univariate analyses of variance to determine which variables were responsible for the differences between species (McPeek 2004). The *F*-approximation of Wilks's λ are presented for the multivariate ANOVA results (Sokal and Rohlf 1995). Lethal contact (LC) and search efficiency (SE) indices were compared with χ^2-test.

Results

Preimaginal development

No differences between *H. axyridis* and *C. maculata* were observed for total survival (*H. axyridis*: 80.0%; *C. maculata*: 86.7%; $\chi^2 = 1.05$, df = 1, $P = 0.31$), adult emergence from pupae (*H. axyridis*: 92.3%; *C. maculata*: 100%; $\chi^2 = 1$, df = 1, $P = 0.32$) and growth index (*H. axyridis*:

4.54%/days; *C. maculata*: 4.28%/days; $\chi^2 = 1$, df = 1, $P = 0.32$).

Developmental time of *H. axyridis* was shorter than *C. maculata* for the eggs ($F_{1,24} = 21.30$, $P < 0.0001$), for the 2nd larval instar ($F_{1,23} = 13.22$, $P = 0.001$) and for the 3rd larval instar ($F_{1,23} = 4.49$, $P = 0.045$) (Figure 1). The developmental time from eggs to 4th larval instar was also shorter for *H. axyridis* than *C. maculata* ($F_{1,23} = 14.09$, $P = 0.001$) (Figure 1). The pupation time was longer for *H. axyridis* than *C. maculata* ($F_{1,23} = 25.50$, $P < 0.001$) (Figure 1). The total preimaginal developmental time of egg to adult of *H. axyridis* was however not significantly different from *C. maculata* ($F_{1,23} = 3.55$, $P = 0.070$) (Figure 1).

Predation efficiency

Harmonia axyridis consumed more number of aphids compared to *C. maculata* during the 2nd larval instar ($F_{1,62} = 10.87$, $P = 0.002$), the 3rd ($F_{1,58} = 40.90$, $P < 0.0001$) and the 4th ($F_{1,83} = 44.46$, $P < 0.0001$) (Figure 2a). *Harmonia axyridis* consumed 50% more aphids (185 ± 11.5) than *C. maculata* (91.92 ± 5.06) during the complete development ($F_{1,203} = 7.87$; $P = 0.006$). Relative weight gain of *H. axyridis* was higher in 2nd instar compared to *C. maculata* ($F_{1,62} = 12.60$; $P = 0.001$) (Figure 2b). Relative growth rate (RGR) of *H. axyridis* (0.79 mg/day ± 0.11) during the total development was significantly higher than that of *C. maculata* (0.25 mg/day ± 0.03) ($F_{1,24} = 23.46$, $P < 0.0001$). There was higher conversion efficiency during the 2nd larval instar of *H. axyridis* compared to *C. maculata* ($F_{1,62} = 4.44$; $P = 0.039$) (Figure 2c).

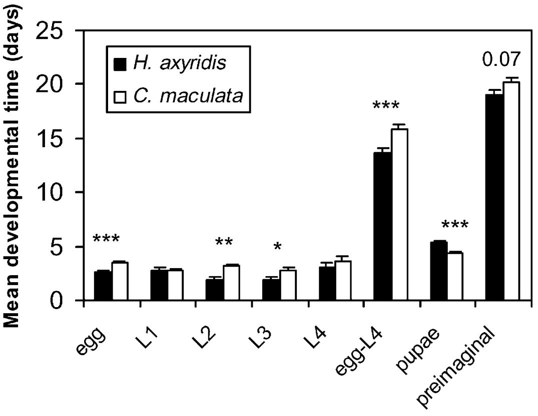

Figure 1. Developmental time (days ± SE) by instars of *H. axyridis* and *C. maculata* on *A. pisum* on broadbean plants. *Note*: $^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

Foraging behavior

Duration of behaviors was significantly different between species and developmental stages (Table 2a). While there were no species differences in the duration of foraging behaviors of 1st, 2nd and 3rd larval instars, there were higher handling (ANOVA, $F_{1,22} = 5.06$, $P = 0.035$) and grooming times (ANOVA, $F_{1,22} = 5.83$, $P = 0.025$) for *H. axyridis* than *C. maculata* in the 4th larval instar (Figure 3a). *Coleomegilla maculata* had longer extensive searching time ($F_{1,22} = 17.13$, $P = 0.001$) as 4th larval instar than *H. axyridis* (Figure 3a).

The whole model of MANOVA was significantly different for the occurrence of behavioral variables between species and stages (Table 2b). There was also a significant interaction between species and stages for the occurrence of behaviors (Table 2b). There were no differences in the occurrence of foraging behaviors of the 1st, 2nd and 3rd larval instars of the two coccinellid species. There was however higher handling occurrence ($F_{1,22} = 10.78$, $P = 0.004$) and higher attacking occurrence ($F_{1,22} = 6.99$, $P = 0.015$) for *H. axyridis* than *C. maculata* in the 4th larval instar (Figure 3b). There was also higher resting occurrence ($F_{1,22} = 10.39$, $P = 0.004$) and higher extensive searching occurrence ($F_{1,22} = 14.11$, $P = 0.001$) for *C. maculata* in this larval instar (Figure 3b).

The lethal contact index was not different between the two species for 1st ($\chi^2 = 0.39$, df = 1, $P = 0.53$), 2nd ($\chi^2 = 0.59$, df = 1, $P = 0.44$) and 3rd ($\chi^2 = 0.13$, df = 1, $P = 0.72$) larval instars. Following an attack, *H. axyridis* was more efficient at killing its prey than *C. maculata* in the 4th larval instar ($\chi^2 = 6.77$, df = 1, $P = 0.009$) (Figure 3c). The search efficiency index was not different between the two species for 1st ($\chi^2 = 0.17$, df = 1, $P = 0.68$), 2nd ($\chi^2 = 0.14$, df = 1, $P = 0.71$) and 3rd ($\chi^2 = 0.99$, df = 1,

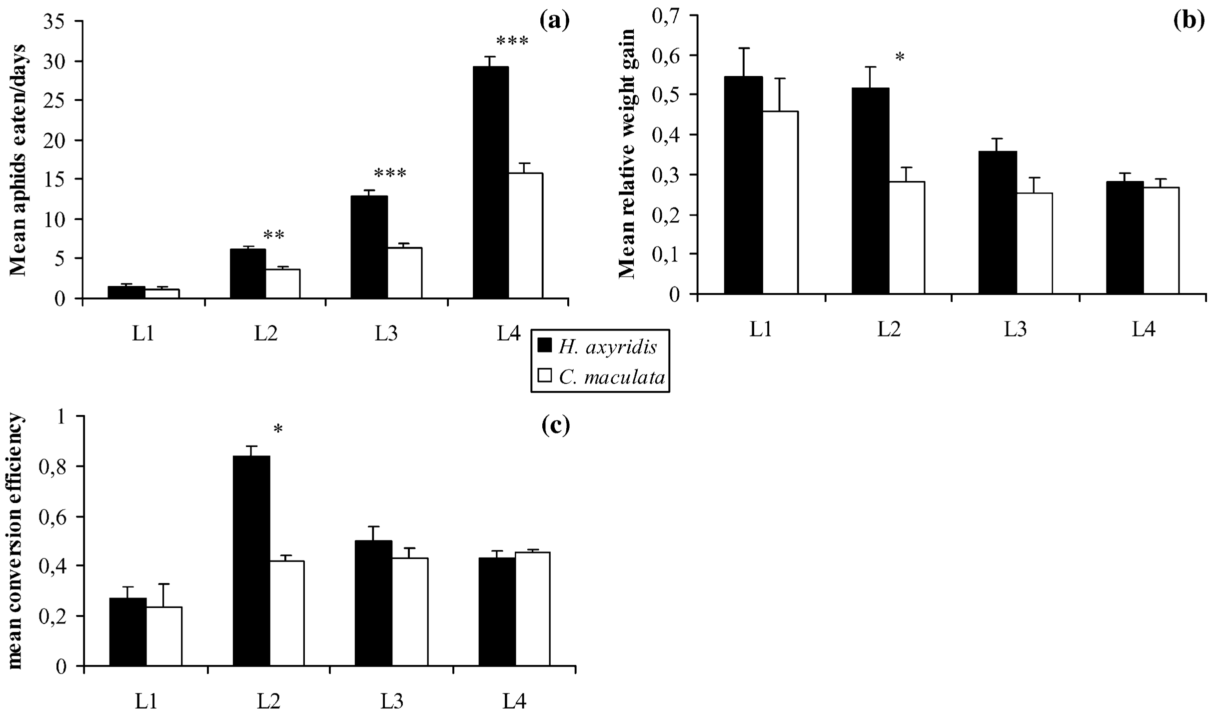

Figure 2. Predation efficiency of each instars of *H. axyridis* and *C. maculata* on *A. pisum* on broadbean plants. (a) Voracity (N aphids/days ± SE). (b) Relative weight gain (mg ± SE). (c) Conversion efficiency (Larval weight (g)/ingested biomass (g) ± SE). *Note*:*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

$P = 0.32$) larval instars. *Harmonia axyridis* was however more efficient in finding its prey than *C. maculata* in the 4th larval instar ($\chi^2 = 7.38$, df = 1, $P = 0.007$) (Figure 3d).

Fifth larval instar

Four individuals (33%) of *H. axyridis* molted to 5th larval instars, but no difference in total

Table 2. Statistical results for MANOVA on time (A) and occurrence (B) of foraging behavior between *H. axyridis* and *C. maculata.*

	Value	Approx. *F*	NumDF	DenDF	Prob > *F*
A					
Whole model					
Wilks' Lambda	0.2257	5.353	36	395.22	< **0.0001**
Species					
F-test	0.1668	4.3777	4	105	**0.0026**
Stages					
Wilks' Lambda	0.2917	9.9782	16	321.42	< **0.0001**
Species × Stages					
Wilks' Lambda	0.8092	1.4413	16	321.42	0.1206
B					
Whole model					
Wilks' Lambda	0.2205	5.4564	36	395.22	< **0.0001**
Species					
F-test	0.4125	10.828	4	105	< **0.0001**
Stages					
Wilks' Lambda	0.3763	7.5748	16	321.42	< **0.0001**
Species × Stages					
Wilks' Lambda	0.6562	2.9299	16	321.42	**0.0001**

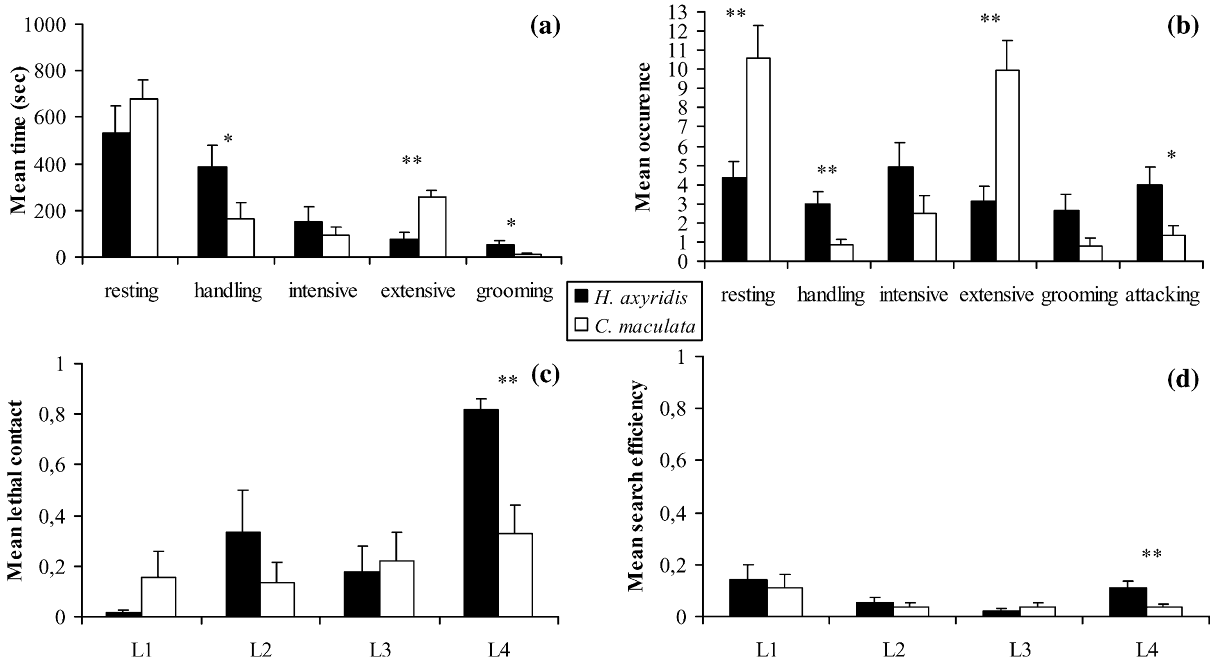

Figure 3. Foraging behaviors of *H. axyridis* and *C. maculata* on broadbean plants after each molt. (a) Mean time (sec ± SE) of behaviors of 4th instar larvae. (b) Occurrence of behaviors (mean ± SE) of 4th instar larvae. (c) Mean lethal contact (number of contact resulting in death of aphids/total contact number) of 4th instar larvae. (d) Mean search efficiency (number of aphids contacted/ total number of aphids on plants) of 4th instar larvae. *Note*: $*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

developmental time of these individuals was observed compared to the other 8 (Wilcoxon test: $z = -0.97$, $P = 0.33$) (Figure 4a). Moreover, preimaginal time development from egg to the last instar (fourth or fifth) was not different between the two groups (Wilcoxon test: $z = -1.67$, $P = 0.095$) (Figure 4a). All individuals of the 5th larval instar were females which exhibited increased voracity (Wilcoxon test: $z = 3.26$, $P = 0.0011$), a greater body mass (Wilcoxon test: $z = 2.54$, $P = 0.011$) (Figure 4b), and an increased weight gain (Wilcoxon test: $z = 3.05$, $P = 0.002$) (Figure 4b) than individuals that completed only a 4th larval instar. Relative weight gain and conversion efficiency were not different between 4th and 5th instar of *H. axyridis*. Duration and frequency of foraging behaviors of 5th instar larvae were not different from the 4th instars. Lethal contact and search efficiency indices of 5th instar larvae were not different from the 4th instar. *Harmonia axyridis* larvae that achieved a 5th larval instar were heavier as adults than larvae that completed a 4th larval instar (Wilcoxon test: $z = 3.67$, $P = 0.0002$) (Figure 4b).

Discussion

Both developmental and behavioral characteristics of *H. axyridis* were different from the indigenous *C. maculata* and may explain the invasiveness of the multicolored Asian lady beetle. We demonstrated a shorter development during the 2nd larval instar, a faster development to the 4th larval instar, and the occurrence of a 5th larval instar for *H. axyridis*. The predation efficiency of *H. axyridis* was higher than *C. maculata*. *Harmonia axyridis* 4th larval instar searched and attacked prey more efficiently than *C. maculata*.

Despite no significant difference in the total preimaginal developmental time (but $P = 0.07$), several interesting differences between the two coccinellid species were observed. *Harmonia axyridis* developed more rapidly during the 2nd

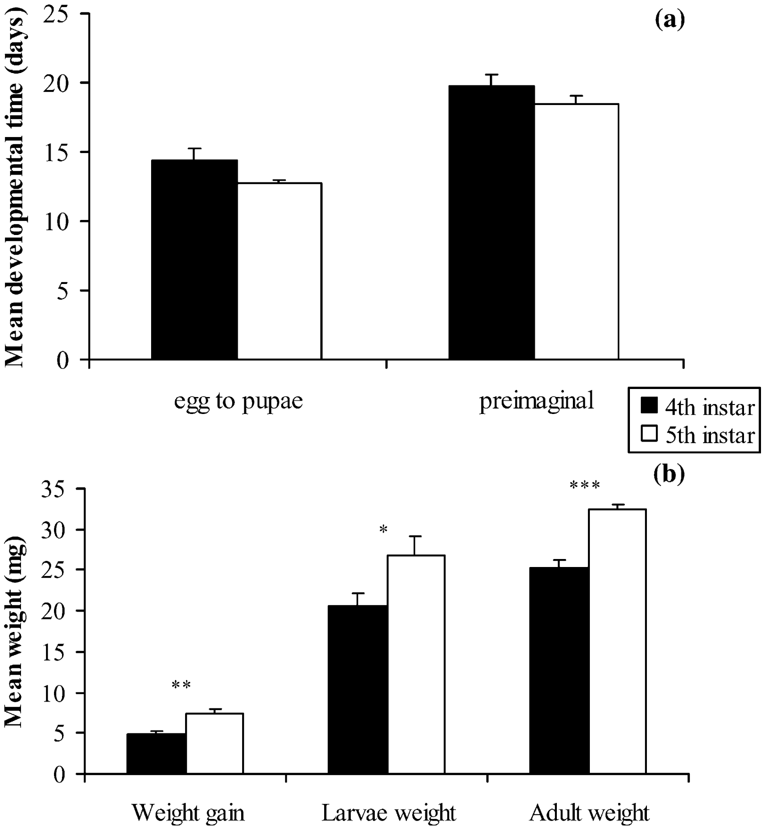

Figure 4. Developmental characteristics of the 5th instars of *H. axyridis* compared to the 4th. (a) Developmental time (days ± SE). (b) Mean weight gain, larvae and adult weight (mg ± SE). *Note*: $*P <$ $** P < 0.01$, $*** P < 0.001$.

larval instar and reached the 4th instar faster than *C. maculata*. Young coccinellid larvae of 1st and 2nd instar cannot actively defend themselves against predation (Hodek and Honek 1996; Lucas et al. 1997b; 1998; Lucas 2005). Cannibalism and intraguild predation cause significant mortality at these young instars, particularly for *H. axyridis*, which experience a relatively high incidence of cannibalism (Burgio et al. 2002; Michaud 2003). A faster development to 3rd and 4th instar should increase survival chances and consequently give an advantage for the individuals that came rapidly through this vulnerable stage. *Harmonia axyridis* attained also more rapidly the 4th instar, which is characterized by strong predation activities (Yasuda and Ohnuma 1999; Yasuda et al. 2001; Lanzoni et al. 2004). This factor, coupled with the reduction of vulnerability of 2nd instars may constitute an advantage for the exotic species. This experiment did not show, however, a more rapid preimaginal developmental time for *H. axyridis* compared to the indigenous species. This result appears also in the experiment of Lanzoni et al. (2004) in Italy when they compared *H. axyridis* with the indigenous species *Hippodamia variegata* (Goeze) and *Adalia bipunctata* (L.). Pupation time of *H. axyridis* was longer than *C. maculata* and can explain lack of difference in the preimaginal developmental time. The pupation is another vulnerable stage during development in ladybeetles, but with lower vulnerability than first instars because they pupate in retired places, with lesser chances to be found and consumed or parasitized and with their ability to flick up and down (Majerus 1994; Lucas et al. 2000). Simultaneously obtaining enough food to grow and reproduce while avoiding predation is a pervasive trade-off faced by many organisms

(McPeek 2004). *Harmonia axyridis* seems to perform this trade-off with its developmental pattern and this could explain its invasive success.

Confirming our second hypothesis, *H. axyridis* presented greater predation efficiency than *C. maculata*. *Harmonia axyridis* consumed significantly more pea aphids than *C. maculata* during almost all instars. Furthermore, relative growth rate during preimaginal development was higher for *H. axyridis*, indicating that the invasive species can accumulate higher biomass in a shorter period of time than the native species. This may facilitate exploitation of pests with rapid population fluctuations such as aphid outbreak (Schellhorn and Andow 1999). Weight gained by each species is determined by its physiological ability to convert assimilated food into its own biomass (Dixon and Hemptinne 2001). Large ladybird beetles need less biomass of aphids per unit area for satiation than do small ladybird beetles because of higher searching efficiency (Dixon and Stewart 1991). It follows that larger ladybird beetles will have higher conversion efficiency and thus require a lower amount of aphid biomass to develop (Dixon and Stewart 1991; Kozlowski and Weiner 1997). Conversion efficiency of *H. axyridis* was higher than *C. maculata* in 2nd larval instar. Higher conversion efficiency in 2nd instar can explain the faster developmental time and would give a strong advantage to the invasive species to avoid predation during this vulnerable stage. Higher resource conversion efficiency can also increase exploitative competition ability and increase population density of the invading species (Byers 2000). *H. axyridis* benefits from both these mechanisms.

Behavioral observations of coccinellid larvae confirmed higher predatory efficiency of *H. axyridis* as 4th instar than *C. maculata*. It is thought that a more efficient predator attacks a larger proportion of prey population over a given period of time (Dixon 2000). Lethal contact proportion of *H. axyridis* as 4th instar on pea aphids is more than two-times superior (81.5 ± 4.7%) than *C. maculata* (32.7 ± 11.2%), indicating that when an aphid is detected, it is almost always killed and eaten by the multicolored Asian lady beetle. *Harmonia axyridis* adults have a high ability to track aphid populations in space and time (Osawa 2000; With et al. 2002). Search efficiency of *H. axyridis* as 4th instar on pea aphids (11.1 ± 2.2%) was more than three-times superior than *C. maculata* (3.5 ± 1.1). Fourth larval instars of *H. axyridis* are also characterized by a lower frequency and duration of extensive searching, but with an increased number of attacks on aphids, an increased lethal contact proportion and searching efficiency on aphids than *C. maculata*. These factors confirmed that *H. axyridis* is a more efficient predator than *C. maculata* in the 4th larval instar.

Fifth larval instars may also promote invasion of *H. axyridis*. Only three coccinellid species were mentioned in the literature having performed 5th larval instars, *C. maculata*, *Chilocorus bipustulatus* L. and *Callicaria superba* Mulsant (Warren and Tadic 1967; Majerus 1994; Hodek and Honek 1996). Normally, when a 5th larval instar is found in coccinellids, the supposition is that the juveniles have experienced relatively low quality of food and they present a decreased growth rate or adult size (Warren and Tadic 1967; Hodek and Honek 1996). In our case, individuals with a 5th larval stage developed at the same rate, consumed more aphids and weighted more than other conspecific larvae. Furthermore, adults with 5 instars were heavier than those with 4. Weight of adult coccinellids is positively correlated with reproductive capacity (Stewart et al. 1991; Dixon 2000). Therefore, we can suppose that higher weight of 5th larval instar can generate higher reproductive capacity to *H. axyridis*. Occurrence of a 5th larval instar that performed better in the new environment gave a strong advantage for an invasive species that should achieve a higher fecundity and higher population. The occurrence of this 5th larval instar can be a genetic or a phenotypic change following the introduction. Some studies have shown that species may attain dominance in introduced ranges because they experience rapid genetic changes linked to new selection pressures in the novel environment (Blossey and Nötzold 1995; Sakai et al. 2001; Lee 2002; Hänfling and Kollman 2002; Stockwell et al. 2003; Hierro et al. 2005). The evolution of increased competitive ability (EICA) hypothesis (Blossey and Nötzold 1995) argues that exotics liberated from their specialist enemies should lose costly traits that confer resistance to their native specialist enemies. Exotics can reallocate resources from the maintenance of resistance to traits, such as size or fecundity, which might be under greater selection in the introduced range (Hierro et al. 2005). Thus, EICA predicts that liberation from natural enemies should result in exotics evolving in ways that enhance their performance in new communities. In the case of *H. axyridis*, the occurrence of a 5th larval instar, that give some advantage in body size and in fecundity, can be such genetic change. It seems that there is no effective parasitism by *Dinocampus coccinellae* Shrank (Firlej et al. 2005) in Quebec, a parasitoid of many coccinellid species commonly found in Asia and in North America. This coccinellid species seem almost free from predation pressure in our area. The EICA hypothesis can be considered for the multicolored Asian lady beetle. Other hypothesis could also be envisaged to explain the occurrence of a 5th instar such as the bet-hedging strategy or the phenotypic plasticity (West-Eberhard 1989; Scheiner 1993; Dixon 2000; Soula and Menu 2003). Bet-hedging strategy is an adaptation to environmental stochasticity in which more than one phenotype is maintained by a single genotype (Soula and Menu 2003). By contrast, phenotypic plasticity is the variation in the phenotypic expression of a trait induced by environmental conditions, where different adaptative phenotypes are maintained in the same life stage and the same population but not necessarily simultaneously expressed in the same individuals (West-Eberhard 1989; Scheiner 1993; Dixon 2000). Nonetheless, this first observation of the phenomenon in *H. axyridis* warrants further investigation to understand this variation in our area.

The key factors in invasion process are growth of juveniles into the adult stage and survival of adults (Marco et al. 2002). Presence of juveniles in high density could accelerate rate of invasion, and is often accompanied by displacement of native species (Marco et al. 2002). Our study pointed more precisely which developmental characteristics of the multicolored Asian lady beetle can ensure safer growth of juveniles and higher density of adults in the environment. Studies of juvenile characteristics before introduction of biological control agents or after arrival of a new species can improve our knowledge of the invasion process and prediction of successful invaders. Some characteristics such as better searching abilities and faster developmental time in introduced biological control agents had shown positive correlation with non target effects (Kimberling 2004). We demonstrated that all these characteristics were present in the multicolored Asian lady beetle. Some negative impacts on native fauna had been shown after its arrival in North America (Tedders and Schaefer 1994; Brown and Miller 1998; Colunga-Garcia and Gage 1998; Michaud 2002; Reitz and Trumble 2002; Snyder et al. 2004). We can expect nontarget effects of the arrival and spread of this species in our country. Survival of adults is also important in invasion process (Marco et al. 2002). Our study had shown that some larvae presented higher weight in adults and possibility of higher fecundity with the occurrence of a surnumerary larval instar that may ensure higher population growth and density. Survival of juveniles and adults is greatly influenced by habitat invasibility, e.g. different resource availability for the species as food, habitat suitability or quality of overwintering sites (Hierro et al. 2005; Marco et al. 2002). Survival of this species related to competitive ability, winter survival and resources exploitation are currently under study and will make an entire portrait of this invasive species, with better understanding of invasion process.

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