DOI: 10.1111/j.1570-7458.2008.00740.x

Role of prey–host plant associations on *Harmonia axyridis* and *Episyrphus balteatus* reproduction and predatory efficiency

Ammar Alhmedi, Eric Haubruge & Frédéric Francis*

Functional and Evolutionary Entomology, Gembloux Agricultural University, Passage des Déportés 2, B-5030 Gembloux, Belgium

Accepted: 8 April 2008

Key words: host preference, integrated pest management, Coleoptera, Coccinellidae, Diptera, Syrphidae, aphids, wheat, green pea, stinging nettle, hoverflies, ladybirds, tritrophic interactions, spatial distribution

Abstract

In order to predict possible locations of *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) and *Episyrphus balteatus* DeGeer (Diptera: Syrphidae) in the field, we studied their oviposition and prey preferences in relation to several host plant–prey associations under laboratory conditions. Oviposition preference of *H. axyridis* and *E. balteatus* females was determined for three aphid (Homoptera: Aphididae)–host plant associations: *Microlophium carnosum* Buckton on stinging nettle [*Urtica dioica* L. (Urticaceae)], *Acyrthosiphon pisum* Harris on green pea [*Pisum sativum* L. (Fabaceae)], and *Sitobion avenae* F. on wheat [*Triticum aestivum* L. (Poaceae)]. Prey preference of *H. axyridis* and *E. balteatus* larvae was determined with the aphids *M. carnosum*, *A. pisum*, and *S. avenae*. *Harmonia axyridis* females showed a strong oviposition preference for the stinging nettle–*M. carnosum* association. The preferred association for ovipostion by *E. balteatus* was pea-hosting *A. pisum*, on which fecundity was also highest. Feeding behaviour was less restricted in *H. axyridis*, in which the preferred preys were *M. carnosum* and *S. avenae*. A lower specificity of predation was observed in *E. balteatus* larvae with respect to *A. pisum*. These laboratory experiments may help us to understand the spatial distribution of *H. axyridis* and *E. balteatus* in the field.

Introduction

In agroecosystems, the spatial distribution of insect species is determined to a large extent by the oviposition behavior of females, if their larvae have limited dispersal capabilities (Huignard et al., 1986; Hanks, 1999). Oviposition behavior is central to many aspects of insect biology, for example, population dynamics and biological control. Female insects may show a preference for specific host plants as oviposition sites. Such a preference can be influenced by various factors. For example, oviposition preference can be determined by experiences of the female as a larva. This has been demonstrated in some species (Jermy et al., 1968), but not in others (Holopainen, 1989; Ntonifor et al., 1996). Oviposition preference may also be influenced by early adult experience (Traynier, 1984; Jaenike, 1990; Turlings et al., 1993), as experience on a previous host may affect fertility on a subsequent host (Jaenike, 1990; Cunningham et al., 1998). Other factors influencing oviposition preference are competition for sites (Finch & Jones, 1987; Jaenike, 1990; Dicke, 2000), presence of natural enemies (Root, 1973; Ohsaki & Sato, 1994; Dicke, 2000), and distribution of potential host plants (Wiklund, 1982; McLain, 1992; Päts et al., 1997). There is little information about how generalist predators, such as the aphidophagous multicoloured Asian ladybird *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) and the hoverfly *Episyrphus balteatus* DeGeer (Diptera: Syrphidae), decide which kind of prey to consume. Most insects are rather specific when choosing their food (Hodek, 1993; Schoonhoven et al., 1998), and even generalist predators display a hierarchy of preferences for different hosts (Sadeghi & Gilbert, 1999).

Optimal foraging theory assumes that predators select prey in order to maximize their fitness through optimal choices based on the caloric and nutritive value of prey and associated foraging costs (Stephen & Krebs, 1986). Several

---

*Correspondence: E-mail: francis.f@fsagx.ac.be

factors affect prey selection: (i) prey features, such as species (Molles & Pietruszka, 1987; Roger et al., 2000), size (Allan et al., 1987; Roger et al., 2000), mobility (Clements & Harmsen, 1990; Eubanks & Denno, 2000), nutritional quality (Houck, 1991; Eubanks & Denno, 2000), and population density (Jeschke & Tollrian, 2000); and (ii) predator characteristics, such as size (Allan et al., 1987; Erickson & Morse, 1997), age (Sullivan, 1984; Cisneros & Rosenheim, 1997), and feeding state (e.g., Molles & Pietruszka, 1987; Houck, 1991).

Harmonia axyridis is used as a control agent against aphid populations, because its larvae are voracious, polyphagous, and easy to rear (Ferran et al., 1996; Koch, 2003). As an adult, it is known to have strong dispersal capacities (Osawa, 2000; Koch, 2003) and studies in North America have shown that it can rapidly colonize large areas (Tedders & Schaefer, 1994). In Europe, it has spread very rapidly, particularly since 2002, and feral populations of the species now exist in 13 European countries (Brown et al., 2007). Since 1999, the Belgian Ladybird Working Group has mapped all Belgian Coccinellidae and recorded data on substratum plants and habitat. The first feral *H. axyridis* population in Belgium was recorded in 2001, but it has now colonized the whole country. Recorded occupancy in Belgium showed an average rate of increase of 189% between 2002 and 2006 (Adriaens et al., 2008). Laboratory experiments showed that *H. axyridis* is frequently involved in intraguild interactions with other aphidophagous species, such as the ladybird species *Adalia bipunctata* (L.) and *Coccinella septempunctata* L., both native to western Europe (Hironori & Katsuhiro, 1997; Cottrell & Yeargan, 1998; Yasuda et al., 2001). In a previous field study, where *Microlophium carnosum* Buckton, *Sitobion avenae* F., and *Acyrthosiphon pisum* Harris (all Homoptera: Aphididae) were the main aphids recorded in high numbers on stinging nettle, wheat, and pea, respectively, a spatial distribution for *H. axyridis* was found: throughout the observation period, it was most abundant on stinging nettle, less in a pea crop, and absent from a wheat field (Alhmedi et al., 2007).

Several factors may have an impact on the oviposition behavior of aphidophagous ladybirds, such as (i) aphid species (Blackman, 1967; Olszak, 1988; Kalushkov & Hodek, 2004; Provost et al., 2006), (ii) aphid density (Dixon, 1959), (iii) aphid colony age (Dixon, 2000), and (iv) presence of intra- or inter-specific competitors/predators (Mills, 1982; Osawa, 1993; Burgio et al., 2002). Many experiments have demonstrated that aphids are not all equally suitable for the larval growth or adult reproduction of a particular ladybird species (Blackman, 1967; Olszak, 1988; Kalushkov & Hodek, 2004). For example, *C. septempunctata* adults respond differently to the kairomones produced by different aphid species (Sengonca & Liu, 1994). This indicates that females may be able to discriminate between aphid species. If this is the case, females should lay eggs more readily near suitable than moderately suitable or unsuitable aphids.

The larvae of many hoverfly species, such as the common hoverfly *E. balteatus*, are also important natural enemies of aphids (Chambers & Adams, 1986; Tenhumberg, 1995). While *E. balteatus* larvae feed on a wide variety of aphid species, even within a single habitat (e.g., Mizuno et al., 1997), there are clear indications of host preferences. *Episyrphus balteatus* is recorded as being more generalized than other syrphids, such as *Syrphus ribesii* (e.g., Ninomyia, 1957), but typically this species is found in various prey colonies within one habitat (Wnuk, 1972; Mizuno et al., 1997). In the present study, we investigate oviposition and predation preference of *H. axyridis* and *E. balteatus* in relation to host plant–prey associations.

Materials and methods

Plant and insect materials

All aphidophagous predators, aphids, and host plants used in our tests were cultured and reared at 22 ± 2 °C and at L16:D8 photoperiod. Similar climatic conditions were used for all experiments. Culture medium for plant growth consisted of a mix of vermiculite and perlite. Broad bean plants were sown in pots (12 cm in diameter × 10 cm high; 9 seeds per pot) in a culture room. The broad bean aphid, *Megoura viciae* Buckton, mass-reared on potted broad bean in the laboratory, was used as prey for the predator cultures.

Wheat, pea, and stinging nettle plants were grown in pots (12 cm in diameter × 10 cm high) in a rearing room, and used as host plants for the three aphid species in the oviposition preference experiments. A culture of the cereal aphid, *S. avenae*, obtained from the Walloon Center of Agronomic Research of Gembloux, was established on potted wheat. The pea aphid, *A. pisum*, reared on broad bean plants in the laboratory, was established on potted green pea. The stinging nettle aphid, *M. carnosum*, was collected from a natural area of nettle in Gembloux and cultured on potted stinging nettle in the laboratory. The aphids mentioned here were the main aphid species recorded on nettle, pea, and wheat in fields (Alhmedi et al., 2007).

Multicoloured Asian ladybird adults, *H. axyridis*, were obtained from Eric Lucas' laboratory in Montreal, Canada, reared in an incubator for several generations, at 22 ± 2 °C and L16:D8 photoperiod, and provided with bee-collected pollen, crystalline sugar, and water. Pollen and water were changed once per week and egg batches were collected regularly. Adults and larvae were fed with *M. viciae* aphids and reared on broad bean leaves and pollen in boxes of 10 × 30 × 10 cm.

The native hoverfly *E. balteatus* was cultured in wooden cages (60 × 100 × 100 cm) with a sliding door. Adults were maintained in a constant environment of 22 ± 2 °C and L16:D8 photoperiod, and they were provided with bee-collected pollen, crystalline sugar, and water. Pollen and water were refreshed every 2 days. In the mass culture, adult females were stimulated to oviposit by presenting pots of broad bean infested with *M. viciae*. A batch of eggs that was laid over a 2–3-h period provided a cohort of flies with synchronous larval emergence within 48–72 h. Emerged larvae were fed with *M. viciae* cultured on broad bean.

Oviposition preference of *Harmonia axyridis* and *Episyrphus balteatus*

Oviposition preference experiments were performed in the laboratory with 4-week-old adult females of *H. axyridis* and *E. balteatus*. The fertility of all females used was assessed 3 days prior to the preference test by counting the eggs laid on pots of broad bean infested with *M. viciae*. All *H. axyridis* (1 day before ovipositional tests) and *E. balteatus* females (3 days before ovipositional tests) used had no previous exposure to aphids. Oviposition preference of adult females was tested in single- and dual-choice experiments. Three aphid/host plant associations (namely, wheat with *S. avenae*, pea with *A. pisum*, and stinging nettle with *M. carnosum*; in short ‘plant + aphid’) were offered. Ten replicates were run simultaneously for each test. Great care was taken to ensure that all replicate plants were the same size and contained the same number of aphids (200 aphids per plant).

Non-choice experiment. One day after the start of aphid infestation, a single gravid female was introduced into a plastic bottle (9 cm in diameter × 25 cm high), containing the potted plant + aphids. Eggs laid after 2 and 24 h were recorded in each replicate.

Dual-choice experiment. One day after the start of aphid infestation, a single gravid female was introduced into a cage (25 × 25 × 35 cm), containing two different potted plants and aphids. Eggs laid after 2 and 24 h were recorded in each replicate.

Predation preference of *Harmonia axyridis* and *Episyrphus balteatus* larvae

Second instars of *H. axyridis* and *E. balteatu*s were starved overnight before their predation preference was tested in dual-choice experiments, using the three aphid species as prey. Twenty aphid individuals per species were offered in a Petri dish (9 cm in diameter). Ten replicates were run simultaneously for each test. Aphids eaten were recorded after 2, 6, and 24 h.

Statistical analysis

The results of the experiments were analyzed using Minitab 15 and SAS (SAS Institute, 1998). Prior to the analyses, data were checked for equal variances and normality, and log(n + 1) transformed if necessary. Oviposition rates of *H. axyridis* and *E. balteatus* females (non-choice) for plant + aphid were analyzed using one-way analysis of variance (ANOVA). Student–Newman–Keuls tests were run to compare the means among treatments. Data on preference were analyzed using χ^2-test.

Results

Oviposition preference of *Harmonia axyridis* and *Episyrphus balteatus*

Non-choice experiment. Without an alternative option, *H. axyridis* females oviposited more on aphid-infested nettle than on other plants after 2 h (ANOVA: $F_{2,27} = 11.58$, $P<0.001$). From 2–24 h after start, egg numbers did not differ among plants ($F_{2,27} = 2.92$, $P = 0.071$). For *E. balteatus*, there was no significant difference ($F_{2,27} = 1.87$, $P = 0.173$) in the number of eggs laid after 2 h, but from 2–24 h after the start of the experiment more eggs were laid on aphid-infested pea ($F_{2,27} = 10.33$, $P<0.001$) than on either aphid-infested wheat or nettle. Overall, *H. axyridis* laid more eggs on aphid-infested nettle ($F_{2,27} = 16.61$, $P<0.001$) than on either aphid-infested wheat or pea, while *E. balteatus* laid more eggs on aphid-infested pea ($F_{2,27} = 10.97$, $P<0.001$) than on either aphid-infested wheat or nettle (Figure 1).

Dual-choice experiment. After 2 h, *H. axyridis* females had laid more eggs on nettle + aphid than on the other plants ($\chi^2 = 56.0$ for wheat + aphid; $\chi^2 = 26.0$ for pea + aphid; both comparisons: d.f. = 1, $P<0.001$; Figure 2). From 2–24 h, a similar result was obtained: oviposition was highest on nettle + aphid ($\chi^2 = 112.8$ for wheat + aphid; $\chi^2 = 136.0$ for pea + aphid; both comparisons: d.f. = 1, $P<0.001$). Comparing the two least preferred aphid/host plant combinations, oviposition was lowest on wheat + aphid (after 2 h: $\chi^2 = 6.0$, d.f. = 1, $P = 0.014$; 2–24 h: $\chi^2 = 55.7$, d.f. = 1, $P<0.001$).

Episyrphus balteatus females laid significantly more eggs on aphid-infested pea than on wheat + aphid (after 2 h: $\chi^2 = 182.0$; 2–24 h: $\chi^2 = 384.3$; both: d.f. = 1, $P<0.001$) or nettle + aphid (after 2 h: $\chi^2 = 148.9$; 2–24 h: $\chi^2 = 121.6$; both: d.f. = 1, $P<0.001$). After 2 h, oviposition on wheat + aphid and nettle + aphid did not differ ($\chi^2 = 0.02$, d.f. = 1, $P = 0.881$), but from 2–24 h more egges were laid on wheat + aphid ($\chi^2 = 5.2$, d.f. = 1, $P = 0.022$) (Figure 2).

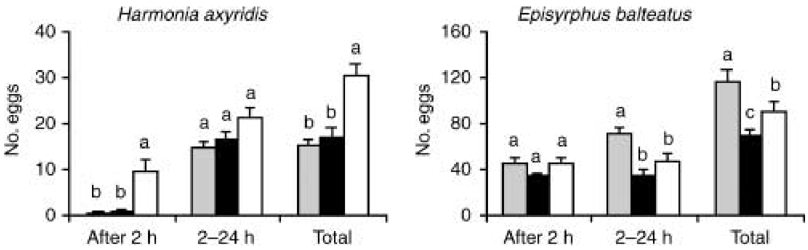

Figure 1 Oviposition rate (mean + SE number of eggs) of *Harmonia axyridis* and *Episyrphus balteatus* in a non-choice experiment according to host plant–prey association (gray bars represent green pea–*Acyrthosiphon pisum* association, black bars represent wheat–*Sitobion avenae* association, and white bars represent stinging nettle–*Microlophium carnosum* association). Bars capped with the same letter during each observation period are not significantly different (one-way ANOVA and Student–Newman–Keuls test: P<0.05).

Predation preference of *Harmonia axyridis* and *Episyrphus balteatus* larvae

Overall, the consumption rate of second instars of *H. axyridis* differed among aphid species: equal numbers of *S. avenae* and *M. carnosum* were consumed ($\chi^2 = 0.4$, d.f. = 1, P = 0.548), but fewer of *A. pisum* (compared with *S. avenae*: $\chi^2 = 85.9$; with *M. carnosum*: $\chi^2 = 45.4$; both: d.f. = 1, P<0.001). Consumption rates varied among observation intervals, where aphids eaten were counted after 2 h (0–2 h), 6 h (2–6 h), and 24 h (6–24 h) (Figure 3). When *M. carnosum* and *A. pisum* were offered simultaneously, *H. axyridis* larvae ate more *M. carnosum* than *A. pisum* during the first and third period of the experiment (after 2 h: $\chi^2 = 13.4$; 6–24 h: $\chi^2 = 20.8$; both: d.f. = 1, P<0.001). *Harmonia axyridis* larvae consumed more *S. avenae* than *M. carnosum* during the first and second period ($\chi^2 = 11.5$, d.f. = 1, P = 0.001 and $\chi^2 = 4.5$, d.f. = 1, P = 0.034, respectively), but more *M. carnosum* than *S. avenae* during the third period ($\chi^2 = 12.4$, d.f. = 1, P<0.001). Ladybird larvae ate consistently more *S. avenae* than *A. pisum* (after 2 h: $\chi^2 = 23.9$; 2–6 h: $\chi^2 = 16.4$; 6–24 h: $\chi^2 = 26.2$; all: d.f. = 1, P<0.001).

Overall, the consumption rate of *E. balteatus* larvae also differed among aphid species: *M. carnosum* was eaten most (compared with *S. avenae*: $\chi^2 = 14.4$, d.f. = 1, P<0.001) and equal numbers of *S. avenae* and *A. pisum* were consumed

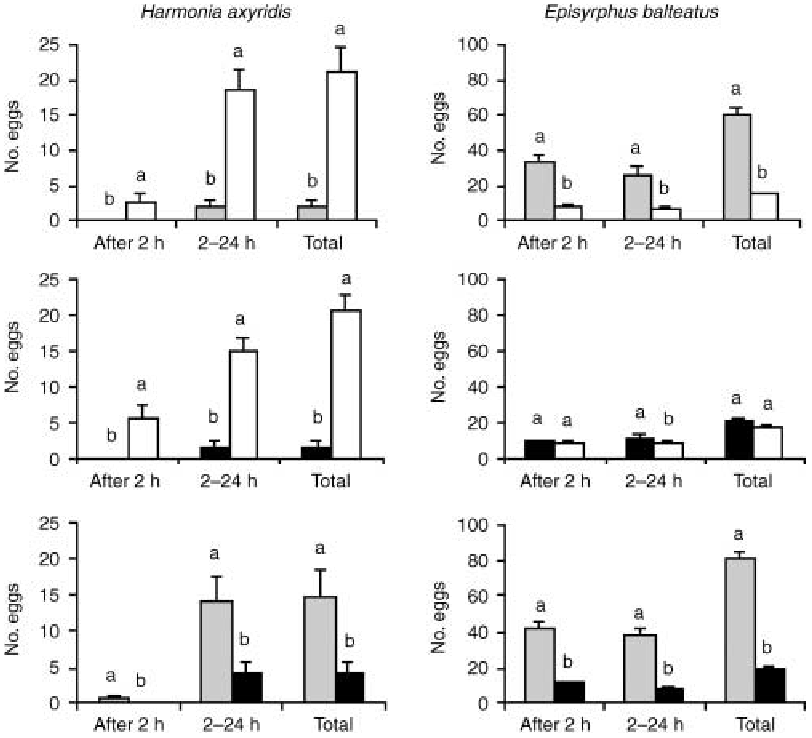

Figure 2 Oviposition preference (mean + SE number of eggs) of *Harmonia axyridis* and *Episyrphus balteatus* in a dual-choice experiment for different host plant–prey associations (gray bars represent green pea–*Acyrthosiphon pisum* association, black bars represent wheat–*Sitobion avenae* association, and white bars represent stinging nettle–*Microlophium carnosum* association). Bars capped with the same letter during each observation period are not significantly different (χ^2-test for observed and expected frequencies, null hypothesis: number of eggs laid is equal in all plants: P>0.05).

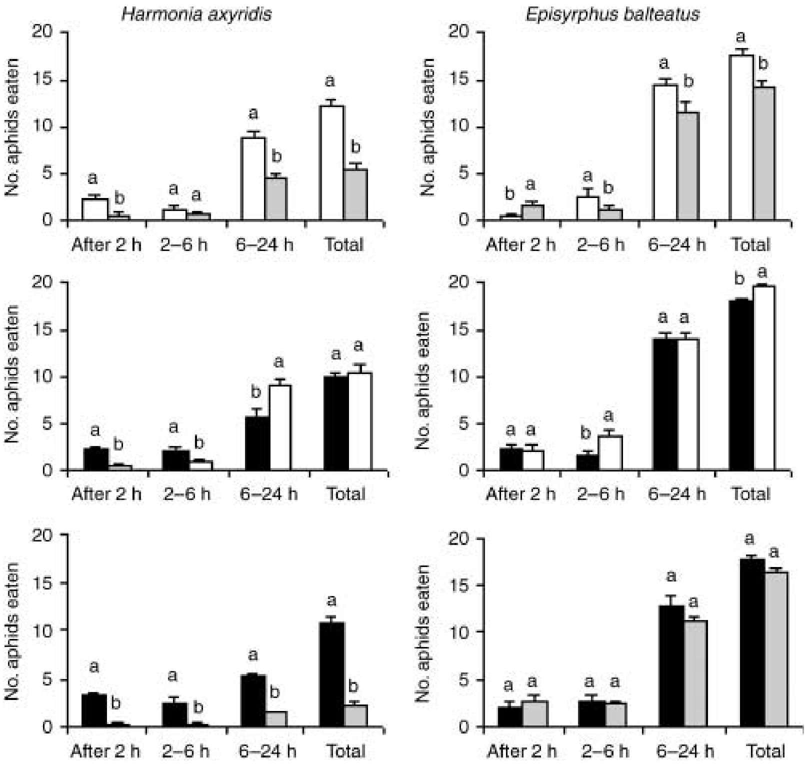

Figure 3 Prey preference (mean + SE number of aphid consumed) of *Harmonia axyridis* and *Episyrphus balteatus* for different aphid species (gray bars represent *Acyrthosiphon pisum*, black bars represent *Sitobion avenae*, and white bars represent *Microlophium carnosum*). Bars capped with the same letter during each observation period are not significantly different (χ^2-test for observed and expected frequencies, null hypothesis: number of eggs laid is equal in all plants: P>0.05).

(χ^2 = 3.8, d.f. = 1, P = 0.050). When *M. carnosum* and *A. pisum* were offered in combination, *A. pisum* was eaten more during the first 2 h (χ^2 = 13.4, d.f. = 1, P<0.001), but thereafter it was eaten less (from 2–6 h: χ^2 = 6.7, d.f. = 1, P = 0.010; 6–24 h: χ^2 = 9.8, d.f. = 1, P = 0.002). During the first and third period, equal numbers of *M. carnosum* and *S. avenae* were consumed. Only from 2–6 h, *M. carnosum* was eaten more (χ^2 = 8.6, d.f. = 1, P = 0.003).

Discussion

When *H. axyridis* and *E. balteatus* females had no choice between aphid/host plant combinations, they oviposited on the plants offered. However, these generalist predators displayed significant differences in egg distribution and prey consumption among the various aphid species. This result supports literature data that suggest selectivity of oviposition (Mitchell, 1962; Niemczyk & Pruska, 1986; Budenberg & Powell, 1992). When *H. axyridis* females were offered a choice, they oviposited preferably on stinging nettle infested with *M. carnosum*, and least on wheat infested with *S. avenae*. Similarly, *H. axyridis* larvae preferred to prey on *M. carnosum*, whereas pea aphid was least eaten. These preferences of *H. axyridis* match with our field observation that this predator was found most often on stinging nettle, and (much) less on pea or wheat (Alhmedi et al., 2007).

Differential consumption rate might be indicative of the ability of *H. axyridis* and *E. balteatus* larvae to differentiate between aphid species, and also shows differences in aphid palatability, which may be due to differences in morphology, behavior, and chemical constitution (Okamoto, 1966; Liepert & Dettner, 1996; Dixon, 2000). The oviposition and consumption preference observed in *H. axyridis* and *E. balteatus* females and larvae in the present study may be explained by optimal foraging theory, which states that the female is likely to select oviposition sites harboring prey that will best support the development and survival of her progeny (Kindlmann & Dixon, 1993).

Females and larvae of *E. balteatus* were found to be less specific in comparison with *H. axyridis*: females preferred *A. pisum* on pea for oviposition, but larvae preferred *M. carnosum* for predation. Previous research by Röder (1990) and Torp (1994) reported *E. balteatus* in equal abundance in all biotypes. This finding also supports field observations by Alhmedi et al. (2007) of similar abundance of *E. balteatus* in different habitats, in association with the occurrence and abundance of aphids. Sadeghi & Gilbert (1999) found that feeding preferences differed among female *E. balteatus*, indicating that part of a population may be specialized, whereas the other part may consist of generalist females.

The oviposition and predation preference of *H. axyridis* observed in the laboratory, as well the specific distribution previously recorded in the field (Alhmedi et al., 2007), may help us to understand its invasion of agroecosystems. For example, the introduction of stinging nettle in pest-management strategies, as shelter for important natural enemies, could lead to undesirable increases of the top predator *H. axyridis* and subsequently enhance the negative interactions with native ladybirds, such as *C. septempunctata* (Yasuda et al., 2004) and *A. bipunctata* (Burgio et al., 2005). However, because *H. axyridis* will likely become permanently established in many of the areas it has invaded, we must continue to advance our knowledge on how to reap benefits in situations where *H. axyridis* is a potential biological control agent and mitigate its effects in situations where it is a potential pest.

In conclusion, although *H. axyridis* is considered a polyphagous ladybird, ovipositing females seem to prefer the stinging nettle–*M. carnosum* complex. Future research is needed to study the orientation of *H. axyridis* movement from nettle zones toward crop field and vice versa. To this end, a laboratory and field study using kairomones for *H. axyridis* will be initiated. The aphid alarm pheromone (*E*)-β-farnesene has already been found to attract *C. septempunctata* (Al Abassi et al., 2000), *A. bipunctata*, and *E. balteatus* (Francis et al., 2001, 2005).

Acknowledgements

We are very grateful to the anonymous reviewers for helpful comments and for English corrections of the manuscript. We thank Prof. Bernard Bodson, Department of Crop Science (FuSaGx) for permission to use the experimental field. We are grateful to Yves Brostaux for help with statistical analyses.

References

Adriaens T, San Martin y Gomez G & Maes D (2008) Invasion history, habitat preferences and phenology of the invasive ladybird *Harmonia axyridis* in Belgium. BioControl 53: 69–88.

Al Abassi S, Birkett MA, Pettersson J, Pickett JA, Wadhams LJ & Woodcock CM (2000) Response of the seven-spot ladybird to an aphid alarm pheromone and an alarm pheromone inhibitor is mediated by paired olfactory cells. Journal of Chemical Ecology 26: 1765–1771.

Alhmedi A, Haubruge E, Bodson B & Francis F (2007) Aphidophagous guilds on nettle (*Urtica dioica*) strips close to fields of green pea, rape and wheat. Journal of Insect Science 14: 411–416.

Allan JD, Flecker AS & McClintock NL (1987) Prey preference of stoneflies: sedentary vs. mobile prey. Oikos 49: 323–331.

Blackman RL (1967) The effects of different aphid foods on *Adalia bipunctata* L. and *Coccinella 7-punctata* L. Annals of Applied Biology 59: 207–219.

Brown PMJ, Adriaens T, Bathon H, Cuppen J, Goldarazena A et al. (2007) *Harmonia axyridis* in Europe: spread and distribution of a non-native coccinellid. Biocontrol 53: 5–21.

Budenberg WJ & Powell W (1992) The role of honeydew as an ovipositional stimulant for two species of syrphids. Entomologia Experimentalis et Applicata 64: 57–61.

Burgio G, Santi F & Maini S (2002) On intra-guild predation and cannibalism in *Harmonia axyridis* (Pallas) and *Adalia bipunctata* L. (Coleoptera: Coccinellidae). Biological Control 24: 110–116.

Burgio G, Santi F & Maini S (2005) Intra-guild predation and cannibalism between *Harmonia axyridis* and *Adalia bipunctata* adults and larvae: laboratory experiments. Bulletin of Insectology 58: 135–140.

Chambers RJ & Adams THL (1986) Quantification of the impact of hoverflies (Diptera: Syrphidae) on cereal aphids in winter wheat: an analysis of field populations. Journal of Applied Ecology 23: 895–904.

Cisneros JJ & Rosenheim JA (1997) Ontogenetic change of prey preference in the generalist predator *Zelus renardii* and its influence on predator-predator interactions. Ecological Entomology 22: 399–407.

Clements DR & Harmsen R (1990) Predatory behavior and prey-stage preference of stigmaeid and phytoseid mites and their potential compatibility in biological control. Canadian Entomologist 122: 321–328.

Cottrell TE & Yeargan KV (1998) Intraguild predation between an introduced lady beetle, *Harmonia axyridis* (Coleoptera: Coccinellidae), and a native lady beetle, *Coleomegilla maculata* (Coleoptera: Coccinellidae). Journal of the Kansas Entomological Society 71: 159–163.

Cunningham JP, Jallow MFA, Wright DJ & Zalucki MP (1998) Learning in host selection in *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae). Animal Behaviour 55: 227–234.

Dicke M (2000) Chemical ecology of host-plant selection by herbivorous arthropods: a multitrophic perspective. Biochemical Systematics and Ecology 28: 601–617.

Dixon AFG (1959) An experimental study of the searching behaviour of the predatory coccinellid beetle *Adalia decempunctata* (L.). Journal of Animal Ecology 28: 259–281.

Dixon AFG (2000) Insect Predator–Prey Dynamics: Ladybird Beetles and Biological Control. Cambridge University Press, Cambridge, MA, USA.

Erickson KS & Morse DH (1997) Predator size and the suitability of a common prey. Oecologia 109: 608–614.

Eubanks MD & Denno RF (2000) Health food versus fast food: the effects of prey quality and mobility on prey selection by a generalist predator and indirect interactions among prey species. Ecological Entomology 25: 140–146.

Ferran A, Niknam H, Kabiri F, Picart JL, Herce CD et al. (1996) The use of *Harmonia axyridis* larvae (Coleoptera: Coccinellidae) against *Macrosiphum rosae* (Hemiptera: Sternorrhyncha: Aphididae) on rose bushes. European Journal of Entomology 93: 59–67.

Finch S & Jones TH (1987) Interspecific competition during host plant selection by insect pests of cruciferous crops. Insects–Plants (ed. by V Labeyrie, G Fabres & D Lachaise), pp. 85–90. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Francis F, Lognay G, Wathelet JP & Haubruge E (2001) Effects of allelochemicals from first (Brassicaceae) and second (*Myzus persicae* & *Brevicoryne brassicae*) trophic levels on *Adalia bipunctata*. Journal of Chemical Ecology 27: 243–256.

Francis F, Martin T, Lognay G & Haubruge E (2005) Role of (E)-β-farnesene in systematic aphid prey location by *Episyrphus balteatus* larvae. European Journal of Entomology 102: 431–436.

Hanks LM (1999) Influence of the larval host plant on reproductive strategies of cerambycid beetles. Annual Review of Entomology 44: 483–505.

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

Hodek I (1993) Habitat and food specificity in aphidophagous predators (a review). Biocontrol Science and Technology 3: 91–100.

Holopainen JK (1989) Host plant preference of the tarnished plant bug *Lygus rugulipennis* Popp. (Het., Miridae). Journal of Applied Entomology 107: 78–82.

Houck MA (1991) Time and resource partitioning in *Stethorus punctum* (Coleoptera: Coccinellidae). Environmental Entomology 20: 494–497.

Huignard J, Thibout E & Biemont J-C (1986) Synchronisation of the reproductive cycle of some phytophagous insects by their host plant. Its adaptative significance. Advances in Invertebrate Reproduction, Vol. 4 (ed. by M Porchet, J-C Andries & A Dhainaut), pp. 425–432. Elsevier Science Publishers, Amsterdam, The Netherlands.

Jaenike J (1990) Host specialization in phytophagous insects. Annual Review of Ecology and Systematics 21: 243–273.

Jermy T, Hanson FE & Dethier VG (1968) Induction of specific food preference in Lepidopterous larvae. Entomologia Experimentalis et Applicata 11: 211–230.

Jeschke JM & Tollrian R (2000) Density-dependent effects of prey defences. Oecologia 123: 391–396.

Kalushkov P & Hodek I (2004) The effects of thirteen species of aphids on some life history parameters of the ladybird *Coccinella septempunctata*. Biocontrol 49: 21–32.

Kindlmann P & Dixon AFG (1993) Optimal foraging in ladybird beetles (Coleoptera: Coccinellidae) and its consequences for their use in biological control. European Journal of Entomology 90: 443–450.

Koch RL (2003) The multicolored Asian lady beetle, *Harmonia axyridis*: a review of its biology, uses in biological control, and non-target impacts. Journal of Insect Science 3: 32–47.

Liepert C & Dettner K (1996) Role of cuticular hydrocarbons of aphid parasitoids in their relationship to aphid attending ants. Journal of Chemical Ecology 22: 695–707.

McLain DK (1992) Oviposition site preference in *Neacoryphus bicrucis* (Hemiptera: Lygaeidae): responses to the density and dispersion of a single host-plant species. Journal of Insect Behaviour 5: 729–739.

Mills NJ (1982) Voracity, cannibalism and coccinellid predation. Annals of Applied Biology 101: 144–148.

Mitchell RG (1962) Balsam woolly aphid predators native to Oregon and Washington. Technical Bulletin of the Oregon Agricultural Experiment Station 62: 1–63.

Mizuno M, Itioka T, Tatematsu Y & Ito Y (1997) Food utilization of aphidophagous hoverfly larvae (Diptera: Syrphidae, Chamaemyiidae) on herbaceous plants in an urban habitat. Ecological Research 12: 239–248.

Molles MC & Pietruszka RD (1987) Prey selection by a stonefly: the influence of hunger and prey size. Oecologia 72: 473–478.

Niemczyk E & Pruska M (1986) The occurrence of predators in different types of colonies of apple aphids. Ecology of Aphidophaga, Vol. 2 (ed. by I Hodek), pp. 303–310. Academia, Prague, Czechoslovakia.

Ninomyia E (1957) On the food habits of some aphidophagous syrphid larvae II. Japanese Journal of Applied Entomology and Zoology 1: 186–192 (in Japanese, English abstract).

Ntonifor NN, Jackai LEN & Ewete FK (1996) Influence of host plant abundance and insect diet on the host selection behavior of *Maruca testulalis* Geyer (Lepidoptera: Pyralidae) and *Riptortus dentipes* Fab (Hemiptera: Alydidae). Agriculture, Ecosystems and Environment 60: 71–78.

Ohsaki N & Sato Y (1994) Food plant choice of *Pieris* butterflies as a trade-off between parasitoid avoidance and quality of plants. Ecology 75: 59–68.

Okamoto H (1966) Three problems of prey specificity of aphidophagous coccinellids. Ecology of Aphidophagous Insects (ed. by I Hodek), pp. 45–46. Academia, Prague, Czechoslovakia/Dr W Junk, The Hague, The Netherlands.

Olszak RW (1988) Voracity and development of three species of Coccinellidae preying upon different species of aphids. Ecology and Effectiveness of Aphidophaga (ed. by E Niemczyk & AFG Dixon), pp. 47–53. SPB Academic Publishing, The Hague, The Netherlands.

Osawa N (1993) Population field studies of the aphidophagous ladybird beetle *Harmonia axyridis* (Coleoptera: Coccinellidae): life tables and key factor analysis. Researches in Population Ecology 35: 335–348.

Osawa N (2000) Population field studies on the aphidophagous ladybird beetle *Harmonia axyridis* (Coleoptera: Coccinellidae): resource tracking and population characteristics. Popululation Ecology 42: 115–127.

Päts P, Ekbom B & Skovgård H (1997) Influence of intercropping on the abundance, distribution and parasitism of *Chilo* spp. (Lepidoptera: Pyralidae) eggs. Bulletin of Entomological Research 87: 507–513.

Provost C, Lucas É, Coderre D & Chouinard G (2006) Prey selection by the lady beetle *Harmonia axyridis*: The influence of prey mobility and prey species. Journal of Insect Behaviour 19: 265–277.

Röder G (1990) Biologie der Schwebfliegen Deutschlands (Diptera: Syrphidae). Erna Bauer-Verlag, Keltern-Weiler, Germany.

Roger C, Coderre D & Boivin G (2000) Differential prey utilization by the generalist predator *Coleomegilla maculata lengi* according to prey size and species. Entomologia Experimentalis et Applicata 94: 3–13.

Root RB (1973) Organization of a plant–arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). Ecological Monographs 43: 95–124.

Sadeghi H & Gilbert F (1999) Individual variation in oviposition preference, and its interaction with larval performance in an insect predator. Oecologia 118: 405–411.

SAS (1998) SAS, Version 8.1. SAS Institute, Cary, NC, USA.

Schoonhoven LM, Jermy T & van Loon JJA (1998) Insect-Plant Biology. Chapman & Hall, London, UK.

Sengonca C & Liu B (1994) Responses of the different instar predator, *Coccinella septempunctata* L. (Coleoptera: Coccinellidae), to the kairomones produced by the prey and non-prey insects as well as the predator itself. Zeitschrift für Pflanzenkrankheiten und Pflanzenschutz 101: 173–177.

Stephen DW & Krebs JR (1986) Foraging Theory. Princeton University Press, Princeton, NJ, USA.

Sullivan KA (1984) Age-specific profitability and prey choice. Animal Behaviour 36: 613–615.

Tedders WL & Schaefer PW (1994) Release and establishment of *Harmonia axyridis* (Coleoptera: Coccinellidae) in the Southeastern United States. Entomological News 105: 228–243.

Tenhumberg B (1995) Estimating predatory efficiency of *Episyrphus balteatus* (Diptera: Syrphidae) in cereal fields. Environmental Entomology 24: 677–691.

Torp E (1994) Danmarks Svirrefluer. Danmarks Dyreliv Bind 6. Apollo Books, Stenstrup, Denmark.

Traynier RMM (1984) Associative learning in the oviposition behaviour of the cabbage butterfly, *Pieris rapae*. Physiological Entomology 9: 465–472.

Turlings TCJ, Wäckers FL, Vet LEM, Lewis WJ & Tumlinson JH (1993) Learning of host-finding cues by hymenopterous parasitoids. Insect Learning, Ecological and Evolutionary Perspectives (ed. by DR Papaj & AC Lewis), pp. 51–78. Chapman & Hall, New York, NY, USA.

Wiklund C (1982) Generalist versus specialist utilization of host plants among butterflies. Proceedings of the 5th International Symposium on Insect–Plant Relationships (ed. by JH Visser & AK Minks), pp. 181–192. Pudoc, Wageningen, The Netherlands.

Wnuk A (1972) Investigations on the species composition of predaceous Syrphidae (Diptera) occurring in the colonies of aphids on fruit trees and shrubs. (in Polish, English abstr.). Polskie pismo Entomologiczne 42: 235–247.

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

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