

Effects of competition, cannibalism and intra-guild predation on larval development of the European coccinellid *Adalia bipunctata* and the invasive species *Harmonia axyridis*

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Abstract. 1. Resource competition and intra-guild predation (IGP) are important determinants of the structure of aphidophagous guilds. The likelihood and outcome of IGP is influenced by the density of extra-guild prey and the characteristics of the species involved.

2. The nature of intra-guild interactions between alien and indigenous coccinellids often determines the success of coccinellid invasions, as exemplified by *Adalia bipunctata* in Japan and *Harmonia axyridis* in North America and Europe.

3. *Harmonia axyridis* has negatively impinged on indigenous species in its introduced range, and its recent arrival in Britain poses a threat for members of native aphidophagous guilds. IGP and inter-specific competition between *H. axyridis* and British coccinellids are predicted to occur. However, the results of such interactions have been little studied.

4. Here we investigate the effects of different diets, designed to mimic possible conditions in the wild, on the survival, development, and adult size of *H. axyridis* and *A. bipunctata*. Results demonstrate a skew in the consequences of IGP between the two species: the supplementation of a limited aphid diet with non-conspecific eggs leads to a significant advantage for *H. axyridis* in respect of all parameters assessed, but gives no benefit to *A. bipunctata*.

5. We conclude that IGP of *A. bipunctata* by *H. axyridis* will contribute to the spread and increase of *H. axyridis* in Britain.

6. We further conclude that the skewed nature of IGP between *A. bipunctata* and *H. axyridis* at least in part explains the limited spread of *A. bipunctata* in Japan.

Key words. *Adalia bipunctata*, alternative prey, aphidophagous guilds, cannibalism, Coccinellidae, *Harmonia axyridis*, intra-guild predation, invasive species, larval development, resource competition.

Introduction

Aphidophagous guilds have a taxonomically diverse array of members, including representatives from Coccinellidae, Syrphidae, and Chrysopidae, as well as many parasitoid wasps and fungal pathogens. As with all ecological guilds based on a

limited resource, the presence of multiple species in aphidophagous guilds leads to inter-specific competition for their shared prey. The ephemeral nature of aphid populations, both spatially and temporally, makes strong competition particularly likely. In addition, many aphidophagous predators, such as coccinellids, have a somewhat generalist diet and will turn to alternative foods when their usual prey runs scarce (Majerus, 1994; Hodek, 1996). Hodek (1973) describes essential prey as that supporting immature growth, development, and adult reproduction, while alternative prey maintains survival until essential prey items are

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located. Aphidophagous coccinellids are known to accept a range of alternative foods during periods of aphid scarcity, and this may include the immature stages of other aphidophages (Majerus, 1994), an act of intra-guild predation (IGP) (Polis *et al.*, 1989). Cannibalism of eggs and larvae is also a common phenomenon amongst aphidophagous coccinellids (Banks, 1956; Majerus & Majerus, 1997; Dixon, 2000), and sibling egg consumption can be highly beneficial in increasing larval survival before dispersal (Pienkowski, 1965; Majerus & Majerus, 1997; Snyder, 2000). Thus, competition, IGP and cannibalism have a considerable influence on the structure of aphidophagous guilds (Rosenheim *et al.*, 1995; Hironori & Katsuhiko, 1997; Lucas, 2005).

Intra-guild predation occurs when two species that share a host or prey, and may therefore compete, also interact trophically (Polis *et al.*, 1989; Rosenheim *et al.*, 1995). The likelihood of IGP is influenced by the abundance of extra-guild prey and the feeding specificity of the species concerned, while the outcome of such an interaction is often determined by the mobility, size and/or developmental stage of both IG predator and IG prey (Sengonca & Frings, 1985; Rosenheim *et al.*, 1995; Lucas *et al.*, 1998; Phoofolo & Obrycki, 1998; Lucas, 2005). In coccinellids, eggs, younger larvae, and prepupae are particularly vulnerable to predation (Agarwala & Dixon, 1992; Majerus, 1994; Dixon, 2000; Sato & Dixon, 2004). As an adaptation against predation, many coccinellids possess chemical defences in the form of alkaloids produced throughout their life cycle (Pasteels *et al.*, 1973; Hemptinne *et al.*, 2000). It is thought that the cost of ingesting these alkaloids makes IGP unprofitable when the abundance of extra-guild prey is high (Hemptinne *et al.*, 2000). However, in times of aphid shortage, many coccinellids are known to extend their diet to include immature stages of other coccinellid species (Agarwala & Dixon, 1992; Lucas *et al.*, 1998; Obrycki *et al.*, 1998; Yasuda & Ohnuma, 1999; Hemptinne *et al.*, 2000; Sato & Dixon, 2004).

It is thought that co-occurring species are often protected from IGP by each other, either by means of chemical defence, or through behavioural adaptations that reduce the likelihood of encounters (Sato & Dixon, 2004). For example, in Japan, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) and *Coccinella septempunctata brucki* Mulsant (Coleoptera: Coccinellidae) are frequently found together in alfalfa fields (Takahashi, 1989). Although the developmental stages of these species are comparable in size, and thus reciprocal IGP might be expected, laboratory experiments have revealed IGP to be strongly asymmetric in favour of *H. axyridis* (Ware & Majerus, 2008). The resistance of *H. axyridis* to IGP from *C. septempunctata brucki* stems from both the possession of defensive chemicals and robust physical defence structures utilised throughout the larval and pupal stages (Ware & Majerus, 2008). Although *C. septempunctata brucki* is highly susceptible to attack by *H. axyridis*, in the wild, differences in the timing of oviposition [*C. septempunctata brucki* lays its eggs earlier in spring than *H. axyridis* (Takahashi, 1989)] mean that *H. axyridis* rarely encounters eggs and younger larvae of *C. septempunctata brucki* (Sato & Dixon, 2004).

While sympatric species might be expected to possess co-evolved defence strategies against IGP, such co-evolved strate-

gies are unlikely between taxa whose ranges do not overlap. Indeed, the ability of an alien species to exploit native members of a guild, while avoiding exploitation itself, is thought to be important in determining the success of establishment and spread (Sato & Dixon, 2004). Two examples of ladybird introductions serve to illustrate this. The two-spot ladybird, *Adalia bipunctata* (Linnaeus) (Coleoptera: Coccinellidae), was first recorded as being established in Japan in 1994 (Sakuratani, 1994), but has so far shown limited habitat use (Kajita *et al.*, 2000). Several studies have reported an asymmetric relationship between *A. bipunctata* and indigenous coccinellids, with the former constituting the IG prey of native species, such as *H. axyridis* and *C. septempunctata brucki*, which act as IG predators (Kajita *et al.*, 2000; Sato & Dixon, 2004). The authors of both studies suggest that the susceptibility of *A. bipunctata* to IGP by native species is partly responsible for its limited invasive potential. In contrast, the invasion of North American aphidophagous guilds by *H. axyridis* has proved to be extremely successful. *Harmonia axyridis* has been repeatedly imported into North America since 1916 to control pest aphids (Koch, 2003; Roy *et al.*, 2006), but only became established in the wild in the late 1980s (Chapin & Brou, 1991). Since then, it has spread and increased rapidly (Coderre *et al.*, 1995; Dreistadt *et al.*, 1995; Kidd *et al.*, 1995; LaMana & Miller, 1995). A range of negative impacts on native ecosystems have been reported, including predation of non-target species (Koch *et al.*, 2003), competition with native aphidophages (Michaud, 2002) and IGP (Hironori & Katsuhiko, 1997; Cottrell & Yeagan, 1998). Whereas *A. bipunctata* did not impact negatively on native Japanese coccinellids to a significant extent, dramatic declines in North American species have been linked to the establishment of *H. axyridis* (Brown & Miller, 1998; Colunga-Garcia & Gage, 1998; Koch & Galvan, 2008).

The success of *H. axyridis* as a biocontrol agent of aphids in the U.S.A. led to introductions into European countries such as France, Belgium, and the Netherlands, during the 1980s and subsequently (Iperti & Bertand, 2001; Adriaens *et al.*, 2003; Brown *et al.*, 2008a). In September 2004, *H. axyridis* was first sighted in Britain (Majerus *et al.*, 2006a). Experiences in North America provoked fears for British ecosystems centred on aphids, particularly native coccinellids. *Harmonia axyridis* is both a dietary and habitat generalist and is therefore likely to interact with a range of British species, including *A. bipunctata* (Ware *et al.*, 2005; Majerus *et al.*, 2006b; Ware & Majerus, 2008). Indeed, recent field observations and survey data demonstrate that eggs, larvae, pupae, and adults of both species can be found together on deciduous trees in S.E. England, particularly on lime (*Tilia x europaea*) and sycamore (*Acer pseudoplatanus*) (R. Ware and M. Majerus, pers. obs.; Brown *et al.*, 2008b; Harlequin Ladybird Survey and UK Ladybird Survey data). The authors also report field sightings of *H. axyridis* larvae consuming *A. bipunctata* eggs, even when aphids are available (R. Ware and M. Majerus, pers. obs.). However, while both IGP and inter-specific competition between *H. axyridis* and British coccinellids are known to occur in the field, the consequences of these interactions have not yet been considered. Here we investigate the effects of IGP and competition on survival, development, and adult size of *A. bipunctata* and *H. axyridis*.

Materials and methods

Ladybird cultures

Fitness parameters in coccinellids, such as adult size, development time and longevity, are often influenced by an individual's gender (Majerus, 1994; Dixon, 2000). We therefore determined to limit comparisons to those between female ladybirds only. In order to maximise the number of female offspring obtained from each matriline, we selected females that were known to be infected by a male-killing *Spiroplasma* (Entomoplasmatales: Spiroplasmataceae). *Spiroplasma* is present at varying prevalence in indigenous populations of *H. axyridis* in Asia (Majerus *et al.*, 1999), and at moderate prevalence in European *A. bipunctata* populations (Majerus *et al.*, 2000). The vertical transmission of the *Spiroplasma* in both species is typically high (> 0.99) so that almost all progeny that hatch from eggs are female, and so usable for our comparisons.

Larvae were derived from ten breeding pairs of Japanese *H. axyridis* (from Tokyo) and European *A. bipunctata* (from St. Petersburg), in which the female was *Spiroplasma*-infected. As females of both species were infected with male-killing *Spiroplasma*, the authors do not consider infection status to be of relevance in the interpretation of results. Individual pairs were housed in 9-cm Petri dishes and kept in the laboratory at 22 °C under constant light. They were fed excess pea aphids, *Acyrtosiphon pisum* (Harris) (Homoptera: Aphididae), daily, and eggs were collected daily prior to transfer of adults to a clean dish to induce oviposition (Majerus *et al.*, 1989). Egg batches were then transferred to a constant environment room at 22 °C, 35% humidity and LD 14h:10 h. Eggs that were to be provided as food for the larvae came from uninfected laboratory stocks of *H. axyridis* and *A. bipunctata* that had been breeding well for a period of 2–3 weeks.

Experimental protocol

Egg batches from infected females were monitored for hatching, which occurred after approximately 4 days in both species. Neonate larvae were removed from their egg-shells, prior to dispersal, with a single-bristle brush and placed individually in a 5-cm Petri dish. In this way, larvae were prevented from consuming unhatched eggs in their clutch. Thirty larvae of each species were reared on one of four different diets: unlimited aphids (A), limited aphids (B), a mixed diet of limited aphids and conspecific eggs (C), or a mixed diet of limited aphids and non-conspecific eggs (D). Details of these diets are as follows:

A Aphids *ad libitum* daily

B Aphids day 1, starvation days 2 & 3, aphids day 4, starvation days 5 & 6, aphids day 7 etc.

C Aphids day 1, conspecific eggs days 2 & 3, aphids day 4, conspecific eggs days 5 & 6, aphids day 7 etc.

D Aphids day 1, non-conspecific eggs days 2 & 3, aphids day 4, non-conspecific eggs days 5 & 6, aphids day 7 etc.

Diet D is considered analogous to when a low extra-guild prey density experienced in the wild is supplemented with IGP. Diet C acts as a control for comparison with diet D to

consider the different effects on fitness of conspecific and non-conspecific eggs.

The number of eggs to be provided as food in diets C and D were scaled for species of larva, larval instar, and species of egg, on the basis of results from preliminary investigations (Table 1). All eggs used were less than 48 h old and were carefully manipulated using a blunt-mounted entomological pin. Numbers of eggs consumed each day (to the nearest half an egg) were recorded, and any aphid or egg remains from the previous day were removed prior to supplying the new day's food. On days where diet B larvae received no aphids, all aphid remains from the previous day were removed.

All larval ecdyses were recorded daily by noting the presence of a shed skin, which was then removed. Deaths, pupations, and eclosions were recorded. Newly eclosed adults were sexed, and after their elytra had hardened sufficiently to allow manipulation, the maximum pronotal width of each female was measured using digital callipers (to the nearest 0.01 mm), as a measure of adult size that is unlikely to vary over time. Adults were then transferred to clean 9-cm Petri dishes and fed excess aphids daily in preparation for a secondary investigation to consider the effect of diet experienced at the larval stage on female reproductive output (Ware *et al.*, in press).

Statistical analysis

All statistical analyses and manipulations were carried out using Minitab 14, with the exception of Fisher's exact test, which was performed in StatXact 7. Survival rates were compared by analysis of 2 × 2 contingency tables using Fisher's exact tests (FEt). All other data were subjected to non-parametric analysis, as Kolmogorov–Smirnov tests revealed a significant difference from a normal distribution. Kruskal–Wallis (KWt) and multiple pairwise Mann–Whitney *U* tests (MWt) adjusting for ties were used. Alpha values were adjusted according to Bonferroni's correction ($\alpha_B = 0.05/N$) for the number of multiple tests (*N*) used in each case. For egg consumption, diet C was compared with diet D within a species, and diets C and D were compared between species, thus giving a total of four tests. For all other parameters, diets A, B, C, and D were each compared with each

Table 1. Numbers of conspecific and non-conspecific eggs provided at each instar to *Harmonia axyridis* and *Adalia bipunctata* larvae. These numbers were established through pilot tests as being sufficient in that they were not all consumed after 24 h.

Species of larva	Instar	<i>H. axyridis</i> eggs	<i>A. bipunctata</i> eggs
<i>H. axyridis</i>	1	3	5
<i>H. axyridis</i>	2	5	8
<i>H. axyridis</i>	3	7	12
<i>H. axyridis</i>	4	10	15
<i>A. bipunctata</i>	1	2	3
<i>A. bipunctata</i>	2	4	6
<i>A. bipunctata</i>	3	6	9
<i>A. bipunctata</i>	4	8	12

other, giving a total of six tests for each species. Diets are referred to as A/B/C/D in details of statistical tests.

Results

Egg consumption

Egg consumption was compared between diets C and D by analysis of the proportions of eggs consumed out of the total number of eggs provided during the larval period (Fig. 1). Both species consumed a significantly greater proportion of conspecific than non-conspecific eggs provided during the larval stages [MWt: αB (4 tests) = 0.013; $W = 1000$, $P < 0.001$, for *H. axyridis*; $W = 844$, $P < 0.001$ for *A. bipunctata*]. *Harmonia axyridis* consumed a significantly higher proportion of the non-conspecific eggs provided than did *A. bipunctata* [MWt: αB (4 tests) = 0.013; $W = 794$, $P < 0.001$]. There was no significant difference in the proportion of conspecific eggs consumed by the two species [MWt: αB (4 tests) = 0.013; $W = 629$, $P = 0.015$].

Survival

Survival was measured in terms of the proportion of adult ladybirds that eclosed (Fig. 2). Survival was higher on diet A (unlimited aphids) than on diet B (limited aphids) for both species [FET: αB (six tests) = 0.008; $F = 24.7$, $P < 0.001$ for *H. axyridis*; $F = 36.89$, $P < 0.001$ for *A. bipunctata*]. Both species showed similar survival under diet C (limited aphids plus conspecific eggs) compared with diet A [FET: αB (6 tests) = 0.008; $F = 2.54$, $P = 0.138$ for *H. axyridis*; $F = 0.13$, $P \sim 1.00$ for *A. bipunctata*]. However, whereas diet D (limited aphids plus non-conspecific eggs) resulted in similar survival to diet A for *H. axyridis* [FET: αB (six tests) = 0.008; $F = 5.68$, $P = 0.021$], *A. bipunctata* survival

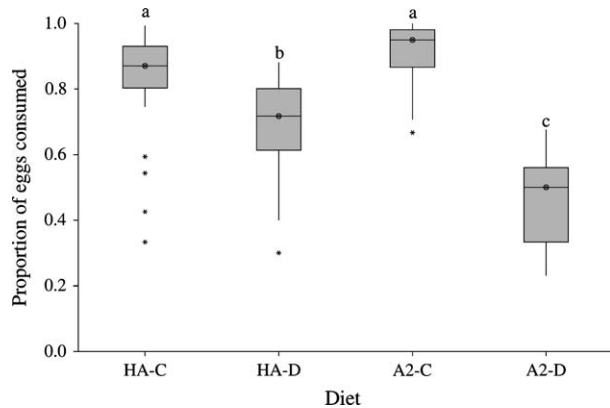


Fig. 1. Proportions of conspecific eggs (C) and non-conspecific eggs (D) consumed by *Harmonia axyridis* (HA) and *Adalia bipunctata* (A2) during the larval stages. Analysis shows that there is no significant difference between results marked with the same lower case letters. Medians (circles with stars), inter-quartile ranges (boxes), ranges (vertical lines) and outliers (stars) are shown.

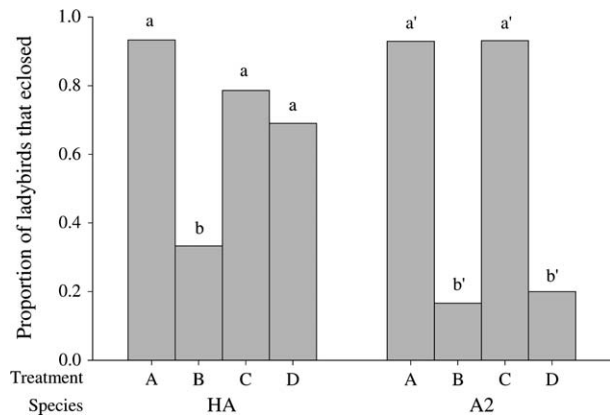


Fig. 2. Survival of *Harmonia axyridis* (HA) and *Adalia bipunctata* (A2) reared on different diets. A = unlimited aphids; B = limited aphids; C = limited aphids plus conspecific eggs; D = limited aphids plus non-conspecific eggs. Analysis shows that there is no significant difference between results marked with the same lower case letters (e.g. 'a' for HA, 'a'' for A2).

was reduced under diet D ($F = 33.7$, $P < 0.001$). Survival was lower under diet B (limited aphids alone) compared with diet C for both species [FET: αB (six tests) = 0.008; $F = 12.04$, $P < 0.001$ for *H. axyridis*; $F = 37.95$, $P < 0.001$ for *A. bipunctata*]. For *H. axyridis*, survival under diet D was higher than under diet B [FET: αB (six tests) = 0.008; $F = 7.42$, $P = 0.008$], but for *A. bipunctata* there was no significant difference in survival between diets B and D ($F = 0.15$, $P \sim 1.00$). There was no significant difference in the number of *H. axyridis* larvae surviving under diets C and D [FET: αB (six tests) = 0.008; $F = 0.68$, $P = 0.550$], but significantly more *A. bipunctata* larvae survived under diet C compared with diet D ($F = 34.71$, $P < 0.001$).

Development

For both species, there was no significant difference in the duration of the pupal stage between the different diets [KWt (A-B-C-D); $H = 5.18$, d.f. = 3, $P = 0.159$ for *H. axyridis*; $H = 1.28$, d.f. = 3, $P = 0.734$ for *A. bipunctata*]. However, the total duration of the larval stage did vary significantly for both species [KWt (A-B-C-D): $H = 61.98$, d.f. = 3, $P < 0.001$ for *H. axyridis*; $H = 39.66$, d.f. = 3, $P < 0.001$ for *A. bipunctata*] (Fig. 3). Larvae of both species developed more quickly on diet A than on any of the other diets [MWt: αB (six tests) = 0.008; *H. axyridis*: A-B: $W = 406.0$, $P < 0.001$; A-C: $W = 409.5$, $P < 0.001$; A-D: $W = 406.0$, $P < 0.001$; *A. bipunctata*: A-B: $W = 302.0$, $P < 0.001$; A-C: $W = 357.0$, $P < 0.001$; A-D: $W = 300.5$, $P < 0.001$]. Larval development time decreased under diet C compared with diet B for both species [MWt: αB (six tests) = 0.008; *H. axyridis*: $W = 211.0$, $P < 0.001$; *A. bipunctata*: $W = 134.5$, $P = 0.006$]. *Harmonia axyridis* larvae developed more quickly on diet D compared with diet B [MWt: αB (six tests) = 0.008; $W = 179.0$, $P < 0.001$], whereas there was no significant difference in development time for *A. bipunctata* larvae reared on diets B and D ($W = 24.5$, $P = 0.600$). There

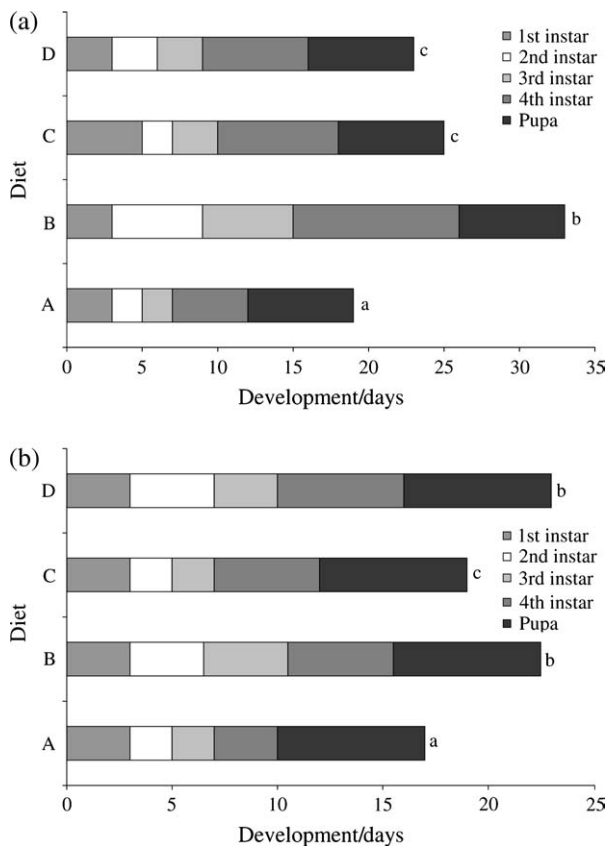


Fig. 3. Median duration of each stage of development from larval hatch to adult eclosion for *Harmonia axyridis* (a) and *Adalia bipunctata* (b) under the four different diets. A = unlimited aphids; B = limited aphids; C = limited aphids plus conspecific eggs; D = limited aphids plus non-conspecific eggs. Analysis shows that there is no significant difference between results marked with the same lower case letters.

was no significant difference in development time of *H. axyridis* larvae reared on diets C and D [MWt: αB (six tests) = 0.008; $W = 387.0$, $P = 0.047$], whereas *A. bipunctata* larvae took significantly longer to develop on diet D ($W = 380.0$, $P = 0.003$).

Adult size

When considering the following results it should be noted that the numbers surviving were low under diet B for both species, and under diet D for *A. bipunctata* (Fig. 2), making the sample sizes analysed small for these groups. Maximum pronotal width of adults varied according to the diet they were fed as larvae [KWt (A-B-C-D): $H = 52.2$, d.f. = 3, $P < 0.001$ for *H. axyridis*; $H = 41.0$, d.f. = 3, $P < 0.001$ for *A. bipunctata*] (Fig. 4). Diet A resulted in larger adult pronotal widths than any of the other diets [MWt: αB (six tests) = 0.008; *H. axyridis*: A-B: $W = 686.0$, $P < 0.001$; A-C: $W = 974.5$, $P < 0.001$; A-D: $W = 941.0$, $P < 0.001$; *A. bipunctata*: A-B: $W = 387.0$, $P = 0.002$; A-C: $W = 847.0$, $P < 0.001$; A-D: $W = 413.0$, $P < 0.001$]. Diet C increased adult pronotal width compared with diet B for *H. axyridis* [MWt: αB (six tests) = 0.008;

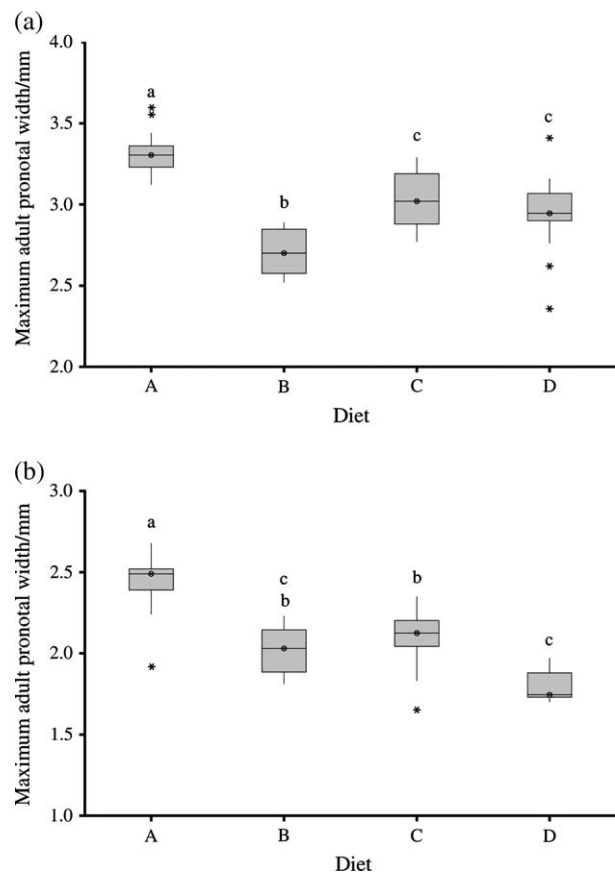


Fig. 4. Maximum pronotal widths of adult *Harmonia axyridis* (a) and *Adalia bipunctata* (b) reared on different larval diets. A = unlimited aphids; B = limited aphids; C = limited aphids plus conspecific eggs; D = limited aphids plus non-conspecific eggs. Medians, inter-quartile ranges and outliers are shown. Analysis shows that there is no significant difference between results marked with the same lower case letters. Medians (circles with stars), inter-quartile ranges (boxes), ranges (vertical lines) and outliers (stars) are shown.

$W = 70.0$, $P < 0.001$) but not for *A. bipunctata* ($W = 55.0$, $P = 0.188$). Diet D resulted in larger *H. axyridis* adults than diet B [MWt: αB (six tests) = 0.008; $W = 80.0$, $P = 0.001$] but, although not statistically significant at the Bonferroni-corrected alpha value, *A. bipunctata* adults reared on diet D seemed to have a slightly shorter pronotal width than those reared on diet B ($W = 42.0$, $P = 0.036$). Accordingly, there was no difference in width of *H. axyridis* adults reared on diets C and D [MWt: αB (six tests) = 0.008; $W = 520.5$, $P = 0.236$], whereas pronotal width of *A. bipunctata* was significantly shorter under diet D ($W = 497.0$, $P = 0.001$).

Discussion

Hodek (1973, 1996) distinguishes between two types of food source utilised by predators. Essential prey supports immature growth, development and adult reproduction, whereas alternative prey merely maintains survival until essential prey is located. The

ability of a species to persist through times of shortage of essential prey will be determined by the effect of the reduction in essential prey intake, and by the consequences of accepting alternative food. In this study, we have considered the effects of larval diet on survival, development, and adult size of *H. axyridis* and *A. bipunctata*. Aphids constitute essential prey for both species, although the range of accepted alternative food sources is much larger for *H. axyridis* (Majerus, 1994; Hodek, 1996; Koch, 2003). The provision of a limited aphid diet is considered analogous to a reduction in essential prey density, and hence increased competition, in the field. The supplementation of a limited aphid diet with conspecific or non-conspecific eggs is therefore representative of the acceptance of alternative foods, either via cannibalism or IGP, respectively.

Both species consumed a higher proportion of conspecific eggs than non-conspecific eggs. The most common predators of coccinellid eggs in the field are larvae of their own species (Majerus, 1994; Dixon, 2000). It is intuitive that the defensive alkaloids present inside coccinellid eggs (Pasteels *et al.*, 1973) will be relatively innocuous to conspecifics – individuals will be able to metabolise or store chemicals that they themselves produce or sequester. Although non-conspecific eggs are considerably less palatable than eggs of conspecifics (Ware *et al.*, 2008), the acceptance of non-conspecific eggs as an alternative food was higher amongst *H. axyridis* larvae than *A. bipunctata* larvae. *Harmonia axyridis* is known to be an extremely generalist predator (Koch *et al.*, 2003; Ware *et al.*, 2005), whereas *A. bipunctata* is an aphid specialist (Majerus, 1994; Ware *et al.*, 2005). This difference in trophic specialisation has also been evident in the field in the U.K., since the authors have observed several instances of *H. axyridis* indulging in cannibalism and IGP of immature coccinellid stages even when aphids are readily available (R. Ware and M. Majerus, pers. obs.).

Results from this work show that larvae developed more quickly and resulted in larger adults when unlimited aphids were provided (diet A), whereas larval development was slowest and smaller adults were produced on the regime of limited aphids alone (diet B). However, survival can be dramatically enhanced by the provision of conspecific eggs alongside limited aphids. In fact, for both species, survival under diet C was close to that under diet A. Thus, conspecific eggs may act as vital alternative prey to allow persistence of the species through times of essential prey shortage, as suggested by other authors (Pienkowski, 1965; Majerus, 1994; Majerus & Majerus, 1997; Dixon, 2000).

Whereas the consumption of conspecific eggs provides an obvious fitness advantage in both species, it seems that the consequences of indulging in IGP of eggs differ significantly between *H. axyridis* and *A. bipunctata*. Survival of *H. axyridis* was increased by the consumption of *A. bipunctata* eggs alongside limited aphids. Conversely, the consumption of *H. axyridis* eggs did not increase *A. bipunctata* survival. Larvae of both species developed more quickly on an unlimited aphid diet and took significantly longer to develop when aphids were limited. The provision of non-conspecific eggs alongside limited aphids considerably reduced development time of *H. axyridis* larvae but had no effect on the development time of *A. bipunctata* larvae. Likewise, adult size was significantly enhanced under diet D for *H. axyridis* but not for *A. bipunctata*. Furthermore, whereas the

provision of non-conspecific eggs to *H. axyridis* larvae had a similar effect on adult size as the provision of conspecific eggs, *A. bipunctata* adults were smaller when given non-conspecific eggs compared with when given conspecific eggs.

It thus seems that the act of intra-guild egg predation, in the context of the species considered here, is of significant adaptive value for *H. axyridis* but provides no benefit for *A. bipunctata* (Table 2). This conclusion is in agreement with other studies demonstrating the ability of *H. axyridis* to successfully exploit other guild members as a food source, while other species are rarely able to exploit *H. axyridis* (Yasuda & Ohnuma, 1999; Burgio *et al.*, 2002; Cottrell, 2004; Sato & Dixon, 2004). Many authors have reported a developmental cost from the consumption of *H. axyridis* eggs by non-conspecific larvae (Burgio *et al.*, 2002; Cottrell, 2004; Sato & Dixon, 2004), although there was no evidence of this in our short-term study (the provision of *H. axyridis* eggs to *A. bipunctata* larvae alongside limited aphids had no effect compared with limited aphids alone, rather than a negative one). It is reasoned that the potential costs of IGP mean that many species will only resort to the consumption of other guild members when they face starvation (Hemphill *et al.*, 2000). For *H. axyridis*, this may not be the case, for the potential long-term fitness advantage of IGP should lead to it occurring routinely when the opportunity arises.

This study has shown that eggs of at least one co-occurring British species constitute a valuable alternative prey for *H. axyridis* and may provide sustenance through times of low essential prey density. Evans *et al.* (1999) report the benefits of a mixed diet containing both essential and alternative prey. Dietary generalism is likely to be extremely important in the persistence of species relying on ephemeral sources of essential food. Members of aphidophagous guilds are frequently faced with shortages in their usual prey, whose populations exhibit extreme density fluctuations in space and time (Dixon, 2000). The ability of *H. axyridis* to capitalise on various alternative food sources, including other members of its guild, is considered partly responsible for its extensive invasion history and disastrous consequences for native species (Koch *et al.*, 2003; Roy *et al.*, 2006). We predict that this ability will also contribute to the spread and increase of the species in Britain. In stark contrast is the limited spread of *A. bipunctata* in Japan, which may be attributable both to its propensity to act as IG prey, and its lower ability to exploit other guild members.

Table 2. Suitability of different diets for growth and development in *Harmonia axyridis* and *Adalia bipunctata*. A = unlimited aphids; B = limited aphids; C = limited aphids plus conspecific eggs; D = limited aphids plus non-conspecific eggs. In this table '>' indicates a more suitable diet and '=' indicates two diets are of equal suitability. Suitability hierarchies are worked out on the basis of the significance of differences observed between diets.

Parameter	<i>Harmonia axyridis</i>	<i>Adalia bipunctata</i>
Survival to adulthood	(A = C = D) > B	(A = C) > (B = D)
Larval development time	A > C > D > B	A > C > (B = D)
Maximum pronotal width	A > (C = D) > B	A > (C = B) > D

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