

# Does the non-native Harlequin ladybird disrupt the feeding behaviour of the native two-spot ladybird?

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## Research Paper

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**Abstract**

Since its arrival in 2004, the non-native Harlequin ladybird *Harmonia axyridis* (Coleoptera: Coccinellidae) has rapidly spread throughout Britain, and it is now the most common coccinellid in England. There have since been concerns about the detrimental effects it may have on native coccinellids because there is a strong correlation between the arrival of *H. axyridis* and the decline in native species, including the two-spot ladybird, *Adalia bipunctata*. However, there have been few studies of the behavioural interactions between these two species, which occupy a high-niche overlap. This study investigated if the presence of *H. axyridis* impacts the feeding behaviour of *A. bipunctata* through direct competition for aphid prey. Foraging and interactive behaviour of *A. bipunctata* and *H. axyridis* were investigated within microcosms. *Adalia bipunctata* exhibited a similar consumption rate and time in the presence of *H. axyridis*, yet *H. axyridis* consumed 3.5 times more prey items and were seven times faster compared to *A. bipunctata*. Observations showed that *H. axyridis* does not directly disrupt the feeding behaviour of *A. bipunctata*, but rather indirectly excludes the native species through being a superior competitor for prey items. Results indicate that the decline in native coccinellid species may be a consequence of *H. axyridis* competitive advantage, but that the concept of coexistence should not be dismissed.

## Introduction

*Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), commonly known as the Harlequin ladybird, multicoloured Asian or Asian ladybird as it originates from Asia, has rapidly spread across Western Europe since its introduction in the 1980s as a biological control agent (Brown *et al.*, 2011; Osawa, 2011). It was first recorded in Britain in 2004 (Majerus *et al.*, 2006), however assessment of the Rothamsted Aphid Trap archive revealed a specimen from 2003 (Roy *et al.*, 2012b). Since its colonization, it has been deemed the ‘most invasive ladybird on earth’ (Roy *et al.*, 2006). Much attention has been focused on *H. axyridis*’s rapid ability to successfully disperse across landscapes; however, hypothesized factors to its success remain largely rudimentary (Alhmedi *et al.*, 2010). The success of *H. axyridis* has been attributed to: (a) its eurytopic nature, thriving in many urban and rural habitats, (b) large climatic tolerance, (c) phenotypic plasticity (d), high dispersal ability, (e) lower susceptibility to pathogens compared to native ladybird species (Roy and Brown, 2015), (f) its generalist feeding behaviour that allows it to exploit a greater range of prey than native coccinellids (Brown *et al.*, 2011). These are typical characteristics of successful invertebrate invasive species (Parker *et al.*, 1999; Snyder and Evans, 2006; Kenis *et al.*, 2008). There is often a strong correlation between the dominance of invasive species and the decline of native species (Roy *et al.*, 2012a) and although a number of studies confirm this, there is a lack of observed interactions (Hentley *et al.*, 2016). An in-depth understanding of the severity of invasive species dynamics is necessary in order to predict future invasions and manage current invaded systems. Moreover, assessments of non-lethal interactive behaviour between invasive and native species may lead to a better understanding of their success (Chapple *et al.*, 2012; Peck *et al.*, 2014).

Invasive predators such as *H. axyridis* frequently compete indirectly with native predators through the consumption of shared prey (Parker *et al.*, 1999; Pell *et al.*, 2007). This alteration in population regulation by natural enemies, across varying trophic guilds, can be seen with aphid communities; a common prey source among coccinellid guilds (Schellhorn and Andow, 2005; Al-Deghairi *et al.*, 2014). However, aphids represent a limited food resource for coccinellids and therefore competitive behaviour can occur. Conversely, competitive exclusion may occur if one predator has a higher consumption rate. This voracity and large body size allow *H. axyridis* to achieve a faster development rate and higher fecundity (Vandereycken *et al.*, 2013).

*Harmonia axyridis* is now the most common coccinellid in England; a pattern seen across much of the world (Comont and Roy, 2011). Their invasion has followed dramatic declines in

several native coccinellid species (Day *et al.*, 1994; Tedders and Schaeffer, 1994; Elliot *et al.*, 1996; Brown and Miller, 1998) and thus, a greater understanding is needed to assess the severity of interactions amongst native coccinellids. The two-spot ladybird, *Adalia bipunctata* (Linnaeus) (Coleoptera: Coccinellidae) is a small, common, generalist predator of aphids in Europe and inhabits a range of environments including urban landscapes and agro-ecosystems (Jalali *et al.*, 2009; Khan *et al.*, 2016). The similarity in both diet and habitat makes the two species likely to interact in the field, and both species can be found together (Harlequin-survey.org, 2018; Ladybird-survey.org, 2018). A 44% decline in the abundance of *A. bipunctata* occurred 5 years after the arrival of the non-native species (Sloggett, 2017), with Roy *et al.* (2012b) suggesting numbers were previously on the increase.

There is relatively little research on the comparative interactions for prey items among coccinellid species (Leppanen *et al.*, 2012), and especially observational assessments of how aphid prey densities influence the intensity of interactions. The aim of this study was to investigate how *H. axyridis* and *A. bipunctata* interact when competing for the same prey resource to help understand why *A. bipunctata* are declining.

## Materials and methods

### Plant and insect cultures

Adults of *H. axyridis* were collected by hand in Fordingbridge, Hampshire and kept in a cold room ( $5 \pm 1^\circ\text{C}$ ) to continue diapause from 2 December 2016 until 30 April 2017. Supplementary stock cultures were kindly donated from Professor Simon Leather, Harper Adams University, Shropshire. Adults of *A. bipunctata* were sourced from biological control suppliers: Green Gardener, Great Yarmouth and Gardening Naturally, Stroud. Both commercial stocks were mixed to reduce any in-breeding. The sex of individuals was not determined as non-destructive certainty is generally difficult (McCornack *et al.*, 2007). 120 beetles were used in total (total  $N$  *A. bipunctata* = 90, total  $N$  *H. axyridis* = 30).

Coccinellid species were contained in separate housing microcosms and transferred to a grow room at  $25 \pm 1^\circ\text{C}$ ;  $55 \pm 5\%$  RH and 16L: 8D. English grain aphids, *Sitobion avenae* (Hemiptera: Aphididae) were provided *ad-libitum*. *Sitobion avenae* used in the experiments were taken from an existing laboratory colony at the Game & Wildlife Conservation Trust, Hampshire.

### Experimental set

To assess how *H. axyridis* affected the feeding behaviour of *A. bipunctata*, a series of feeding trials were conducted. Five Mulika spring wheat, *Triticum aestivum* (Poaceae: Triticum) were grown from seed in 12 plastic pots (12.5 cm diameter  $\times$  13.5 cm height) containing John Innes II compost. Irrigation occurred on rotation using a distilled water source. Clear acetate was fixed around each pot (12.5 cm diameter  $\times$  60 cm height) to confine the wheat plants and a mesh lining was applied at the top to create a microcosm. When the wheat plants had reached ca. 50 cm in height, each of the 12 microcosms was randomly infested with aphids. These were either at low densities (estimated range of 10–60 aphids) or high (estimated range of 70–150 aphids). Aphid abundance in each microcosm was recorded before every feeding trial.

The beetles were kept separately in Petri dishes (9 cm) with a  $1 \text{ cm}^2$  piece of dampened filter paper, and a folded strip of filter paper was provided to act as a substrate for oviposition. Beetles were chosen at random, and of unknown sex and age, for each trial and starved for 24 h. There were two competition treatments with two beetles per microcosm: (1) two *A. bipunctata*, and (2) one *A. bipunctata* and one *H. axyridis* and these were conducted using both aphid densities with three replicates of each competition/aphid density combination per trial. Each trial was repeated ten times using a total of 90 *A. bipunctata* and 30 *H. axyridis*.

For each feeding trial, two of the assigned paired beetles were gently placed on the base of the middle wheat stem within the microcosm using a fine-bristled brush. After the second beetle was placed on the stem, observations were made continuously and terminated after 30 minutes (1800 s). The following activities were recorded: (i) 'location time'; time taken to discover prey (i.e. the first aphid), (ii) 'consumption time'; time taken to consume individual prey, (iii) 'consumption rate'; number of aphids consumed by an individual beetle, and (iv) 'behaviour'; the direct contacts made and perceived response (aggressive/non-aggressive) were noted. Recognised aggressive behaviours of coccinellids were modified from a similar study by Leppanen *et al.* (2012) which assessed competition for aphid prey in laboratory arenas. Behaviours considered as aggressive were categorised as follows: chasing, grasping, biting, climbing upon, and attempting to or successfully stealing prey. Behaviours that were recorded as non-aggressive in the present study included foraging, resting, mandible cleaning and making contact with another individual but not exhibiting an aggressive behaviour as outlined. Feeding trials were conducted in a controlled grow room at  $25 \pm 1^\circ\text{C}$ ;  $55 \pm 5\%$  RH and 16L: 8D from May 2017 to June 2017.

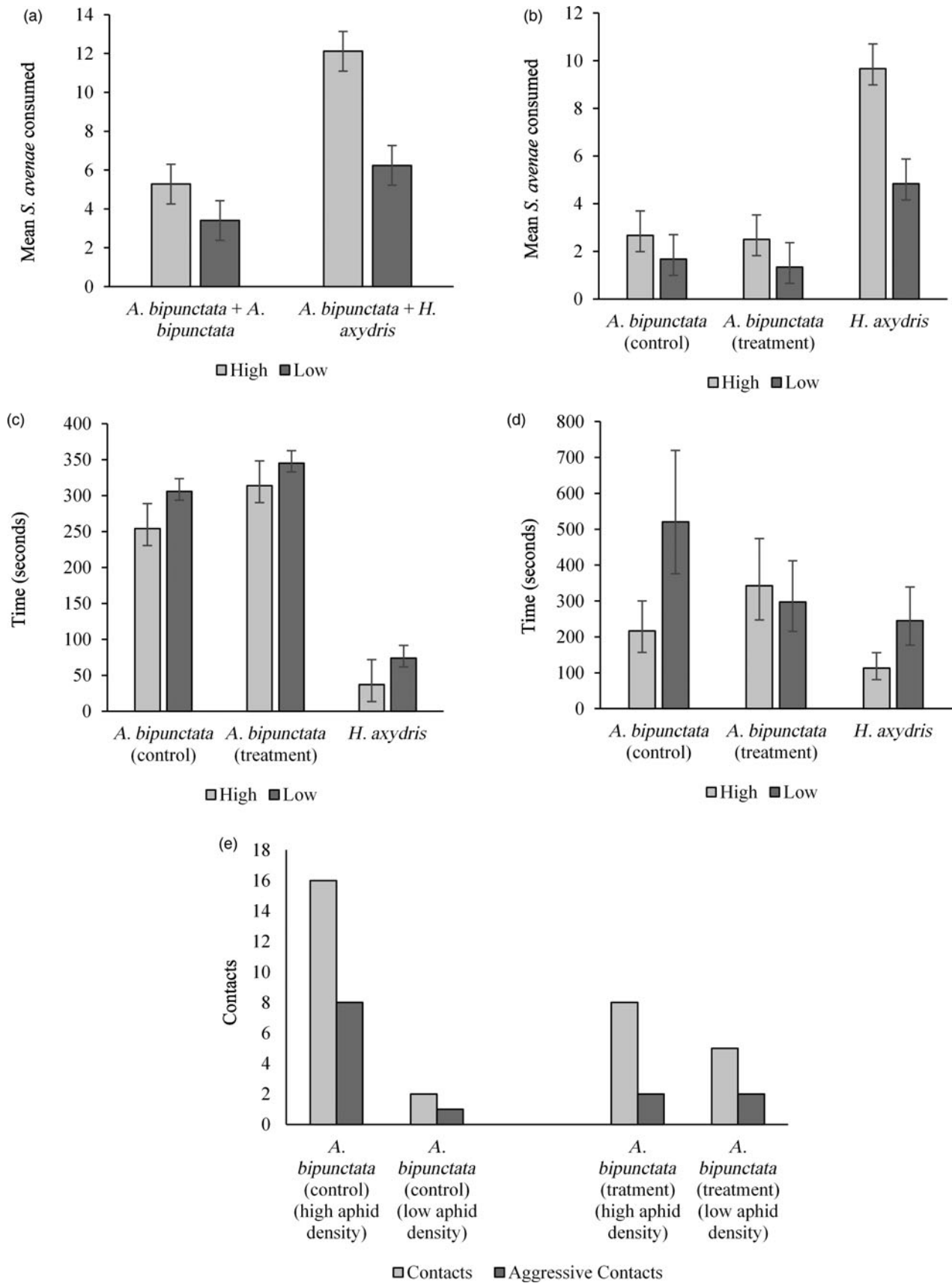
### Statistical analysis

The effect of competition treatment (presence or absence of *H. axyridis*) and aphid density in relation to prey consumption per microcosm was analysed using a two-way analysis of variance (ANOVA). Linear Mixed Models (REML) were used to test whether the number of aphids consumed per beetle species, time taken to locate them and time to consume them differed when *H. axyridis* was present. Three beetle categories were compared: *A. bipunctata* when only beetles of the same species were present, *A. bipunctata* when *H. axyridis* was present and *H. axyridis* alone, and for both aphid densities. Data were transformed ( $\log x + 1$ ) for consumption time and location time before REML was performed. Trial run (1–10) was included as blocking structure in all analyses and tests were run using GenStat (16th edition). An imputed time of 1800 s (30 min) was given to individual beetles that did not locate or consume a prey item, which represented the duration of each feeding trial. Only 31 contacts were observed (aggressive/non-aggressive) which was insufficient for robust statistical analysis into behaviour.

## Results

### Prey consumption

For the total number of aphids consumed, there was a significant interaction effect for competition treatment and aphid density ( $F = 4.29$ ,  $P = 0.044$ ). Higher numbers of aphids were consumed when *H. axyridis* was present in the microcosm for both aphid densities (fig. 1a). However, the difference between the number



**Figure 1.** (a) mean number of *S. avenae* consumed per microcosm under high and low aphid densities between i) control: *A. bipunctata* pairings ii) treatment: *A. bipunctata* and *H. axydris* pairings, (b) mean number of *S. avenae* consumed per beetle species under high and low aphid densities for the three beetle categories (c) mean consumption time per beetle species ( $\pm$ SE) (seconds) of prey items under high and low aphid densities. (d) mean location time per beetle species ( $\pm$ SE) (seconds) of prey items under high and low prey for the three beetle categories, (e) total contacts/aggressive contacts per beetle species between control and treatment pairings under high and low aphid densities.

of aphids consumed for low and high aphid densities was greater when *H. axyridis* was present. A significant interaction effect was also found for the number of aphids consumed per beetle species category and aphid density ( $F = 6.03$ ,  $P = 0.003$ ). *Harmonia axyridis* consumed almost four times more aphids than *A. bipunctata* at the high and three times at the low aphid density (fig. 1b). The number of aphids consumed by *A. bipunctata* was unaffected by the presence of *H. axyridis* and was fewer at the low aphid density.

### Prey consumption time

Consumption time differed significantly between the treatment and control beetle pairings ( $F = 27.68$ ,  $P \leq 0.001$ ) and was unaffected by aphid density. However, consumption time was similar for *A. bipunctata* in the absence ( $2.44 \pm 0.07$ ) and presence of *H. axyridis* ( $2.51 \pm 0.8$ ) (fig. 1c). *Harmonia axyridis* had a shorter consumption time ( $1.58 \pm 0.2$ ) under high aphid densities.

### Prey location time

There was a significant difference between the treatment and control beetle pairings ( $F = 6.24$ ,  $P = 0.003$ ). *Harmonia axyridis* located prey more quickly ( $2.51 \pm 0.01$ ) compared to *A. bipunctata* ( $2.19 \pm 0.01$ ) (fig. 1d). Aphids were also located significantly faster ( $F = 10.27$ ,  $P = 0.002$ ) when present at the higher density, but there was no significant interaction effect, therefore both species were responding similarly.

### Contacts

A total of 31 contacts were observed between control and treatment beetles. More contacts were observed at high than low aphid densities for both beetle species (fig. 1e). The lowest number of aggressive contacts occurred when both beetle species were present at the high aphid density, whereas in all other treatments approximately 50% of contacts were considered aggressive.

A higher proportion of attempts to steal prey was made by conspecifics, and when prey items were not present during a contact, the outcome was often to chase the individual away. There was still chasing behaviour even with the lower frequency of non-aggressive contacts made by heterospecifics, but the majority of initial contacts resulted in avoidance between the treatment pairings. This avoidance strategy could be heightened further if individuals had the ability to fully disperse.

### Discussion

The study revealed an asymmetric competitive interaction between *H. axyridis* and *A. bipunctata* in relation to feeding behaviour. *Harmonia axyridis* was able to locate prey items faster than *A. bipunctata* under high aphid densities, but both species had similar location times with low aphid prey densities. Overall, the number of aphids consumed by *H. axyridis* was always higher regardless of the aphid density; however, this was because their consumption rate was also much faster. This explains why *H. axyridis* are able to outcompete *A. bipunctata* rather than it being through aggressive behaviour, of which there were relatively few incidences. Coccinellids perform an intrinsic array of behaviours to aid in their foraging efficiency (Ferran and Dixon, 1993; Dixon, 2000). To achieve this, an encounter with a prey resource must first occur in order to promote the switch from extensive to intensive search behaviour

(Hodek *et al.*, 2012). *Adalia bipunctata*, in both treatment and control conditions (67%), were witnessed to intensify their foraging efficiency by making erratic, short turns after consumption of an aphid, or indeed when in close proximity to an aphid. This behavioural change was seen in a higher proportion of *A. bipunctata* than *H. axyridis* and could affect their foraging success as they focused on a smaller section of a wheat stem, and thus covered less surface area compared to *H. axyridis*.

The experimental set-up can greatly affect the scope of perceived behavioural response and therefore any interpretation needs an element of caution, especially using confined arenas (Dixon, 2000). Therefore, the faster location time shown by *H. axyridis* in this assay could be higher than normal because of the restriction in dispersal. However, the current experimental assay facilitated a higher level of dispersal compared to previous laboratory studies in which coccinellids were confined to Petri-dishes (Rocca *et al.*, 2017). Furthermore, in natural environments, refuges would exist to prevent competition at plant (Schellhorn and Andow, 2005), field (Hampton, 2004) and landscape levels (Gardiner *et al.*, 2009). This would suggest that when in the presence of heterospecifics, individuals would disperse to avoid competition, and invest energy into profitable activities such as reproduction. This study indicated that coexistence can occur between the two species because there were few aggressive contacts; moreover, the microcosms were sufficiently large to facilitate avoidance and therefore the behavioural responses may reflect natural behaviour.

This study shows that indirect competitive displacement occurs when *H. axyridis* and *A. bipunctata* coexist. *Harmonia axyridis* does not directly exclude *A. bipunctata*'s ability to locate and consume prey items but does show a competitive advantage, and was the more successful aphid predator from the feeding trials. This exploitative competition, which is the most common form of competition amongst arthropod assemblages (Alhmedi *et al.*, 2010), is thought to pose concerns for the population dynamics of the *A. bipunctata* in its native range. In natural environments, there may also be other factors affecting the relationship between the two species, such as habitat complexity and the availability of alternative food resources that yet need to be investigated.

It is certainly apparent that *A. bipunctata* has undergone significant declines in its native range, with *H. axyridis* considered the main cause (Koch *et al.*, 2006; Howe *et al.*, 2015; Sloggett, 2017). Yet, there is evidence spanning 39 years that suggests *A. bipunctata*'s decline occurred before the establishment of *H. axyridis* in Europe (Honek *et al.*, 2017). There is also evidence that aphids have declined substantially during this period and may be responsible (Ewald *et al.*, 2015). Furthermore, *A. bipunctata* has become established in Japan, where it is a non-native species, and coexists among high populations of native *H. axyridis* (Toda and Sakuratani, 2006).

A broader context is therefore necessary in order to underpin declines in native coccinellids, and sole responsibility on the non-native *H. axyridis* should be further revised, along with other driving factors of environmental change.

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