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Effect of intraguild predation on the survival and development of three species of aphidophagous ladybirds: consequences for invasive species

Satoru Sato and Anthony F. G. Dixon

School of Biological Sciences, University of East Anglia, Norwich NR4 7TJ, U.K.

Abstract

1 Survival and development of hatchling larvae of three aphidophagous ladybirds (Coleoptera: Coccinellidae), *Harmonia axyridis* Pallas, *Coccinella septempunctata brucki* Mulsant and *Adalia bipunctata* Linnaeus, when fed their own and the other species eggs were recorded.
2 In all three species, the larvae survived when fed conspecific eggs.
3 The percentage of larvae of *H. axyridis* that survived decreased to 35% and 85% when fed eggs of *A. bipunctata* and *C. s. brucki*, respectively. All the larvae of *A. bipunctata* and *C. s. brucki* died after eating eggs of *H. axyridis*. None of the larvae of *C. s. brucki* died after eating eggs of *A. bipunctata*, whereas 46% of those of *A. bipunctata* died after eating eggs of *C. s. brucki*.
4 In general, larvae were reluctant to eat the eggs of other species. However, larvae of *C. s. brucki* showed less reluctance than *H. axyridis* to eat the eggs of *A. bipunctata*.
5 The consequence of this for invasive species of ladybird is discussed.

Keywords *Adalia bipunctata*, *Coccinella septempunctata brucki*, *Harmonia axyridis*, intraguild predation, species-specific alkaloid.

Introduction

The predators feeding on aphids make up the aphidophagous predator guild. Ladybirds (Coleoptera: Coccinellidae) are very voracious and abundant in terms of numbers of species and individuals and are an important component of these guilds. It is suggested that intraguild predation is important in structuring these guilds (Yasuda & Shinya, 1997).

In general, the outcome of cannibalism and intraguild predation depends on the relative size and/or developmental stage of the prey and predator. Eggs and younger larvae are more vulnerable to cannibalism by older larvae than *vice versa* (Agarwala & Dixon, 1992). Similarly, in intraguild predation, a small species is more likely to be the intraguild prey of a large species (Sengonca & Frings, 1985; Lucas *et al*., 1998; Phoofolo & Obrycki, 1998; Hindayana *et al*., 2001). By implication, small or inactive individuals are likely to be more vulnerable to predation by large or active individual than *vice versa*, irrespective of species.

However, in species of ladybird that have overlapping habitat preferences, small species, such as *Adalia bipunctata* Linnaeus, are more toxic to large species, such as *Coccinella septempunctata* Linnaeus, and this reduces the incidence of the small species being eaten by the large species (Agarwala & Dixon, 1992; Agarwala *et al*., 1998; Hemptinne *et al*., 2000). Thus, vulnerable species may be protected chemically from intraguild predation.

In Japan, *Harmonia axyridis* Pallas and *Coccinella septempunctata brucki* Mulsant commonly coexist in spring (Takahashi, 1989; Yasuda & Shinya, 1997; Sato, 2001). Although all developmental stages of these two species are similar in size, their timing of oviposition relative to the population dynamics of aphids differs; eggs of *C. s. brucki* are more likely to be laid earlier than those of *H. axyridis* (Takahashi, 1989; Yasuda & Shinya, 1997; Sato, 2001). Consequently, *C. s. brucki* is more advanced in its development than *H. axyridis* (i.e. the difference in the timing of oviposition of the two species results in larvae of the latter being physically smaller than the former when they coexist).

Correspondence: S. Sato, Department of Agriculture, Yamagata University, Tsuruoka, Yamagata 997-8555, Japan. Tel: +81 235 282851; fax: +81 235 282851; e-mail: satorus@tds1.tr.yamagata u.ac.jp

If generally vulnerable species are likely to be protected chemically, then *H. axyridis* should be so protected from predation by *C. s. brucki*.

Recently, Sakuratani (1994) reported the first discovery in Japan of *A. bipunctata*, which is a common species in Europe. Intraguild predation of this species by native species of ladybird that have similar habitat preferences, such as *C. s. brucki* and *H. axyridis*, has been reported in the field and laboratory (Kajita *et al.*, 2000; Sakuratani *et al.*, 2000). In addition, *A. bipunctata* and *C. s. brucki*, which is another common species in Japan, are also likely to interact, as *A. bipunctata* and *C. septempunctata* do in Europe (Dixon, 2000). If species-specific toxicity generally affects the incidence of intraguild predation, then such toxicity may determine how successful *A. bipunctata* will be in invading aphidophagous guilds in Japan.

The objective of this study was to determine the toxicity of three ladybirds, *H. axyridis*, *C. s. brucki* and *A. bipunctata*, to one another. The incidence of predation between these species and the likelihood of *A. bipunctata* becoming abundant in Japan is discussed.

Materials and methods

All stages of ladybird contain similar concentrations of alkaloids (Pasteels *et al.*, 1973) that are thought to be responsible for their toxicity. In addition, eggs and hatchling larvae are relatively easy to obtain compared to other developmental stages. Therefore, in this study, the survival and performance of hatchling ladybird larvae fed eggs of their own or the other species were determined.

Females and males of two Japanese ladybirds, *H. axyridis* and *C. s. brucki*, and the European ladybird, *A. bipunctata*, were collected on the campus of Yamagata University, Tsuruoka, Japan and the University of East Anglia, Norwich, U.K., respectively. To obtain eggs, pairs of adults were kept in plastic Petri dishes (9 cm in diameter), each containing a piece of corrugated filter paper, and fed daily with an excess of pea aphids, *Acyrthosiphon pisum* Harris. Any eggs laid on the filter paper were removed and placed in other Petri dishes (9 cm in diameter), and the larvae that hatched from these eggs were each individually transferred within 12 h of hatching to a plastic tube (2.5 cm × 1.0 cm). Each tube had previously been half filled with Plaster of Paris, which was moistened daily with water. To facilitate ventilation, there was a hole in the lid of each tube covered with muslin. The nine treatments were hatchling larvae of *H. axyridis*, *C. s. brucki* and *A. bipunctata*, and were each offered either five of their own, or of one of the other two species eggs, twice a day. The number of eggs eaten was monitored every 12 h when the eggs were replaced and any remaining eggs and egg remains were removed. When counting the number of eggs eaten, an incompletely consumed egg was counted as 0.5 of an egg; those that were almost consumed, or of which only an eggshell remained, were counted as 1.0 egg. This procedure was continued until the larvae moulted to the second-instar or died. All experiments were conducted at 20 °C and LD 16 : 8 h. The treatments, in which larvae of *A. bipunctata* were offered eggs of *H. axyridis* or *C. s. brucki*, were replicated 21 and 26 times, respectively. All other treatments were replicated 20 times. Larvae were recorded as surviving if they moulted to the second instar. The duration of development was the time in days from egg hatch to the moult to the second instar. Average egg consumption was the sum of the eggs consumed during the first instar, or prior to death, divided by duration of first instar or survival in days.

Results

Toxicity was determined by feeding larvae eggs of their own and other species, and recording how many larvae survived to the second instar (Fig. 1), and the results were compared using a chi-square test. In all three species, larvae fed conspecific eggs successfully moulted to the second instar. However, when fed eggs of other species, not all the larvae survived. Approximately half the *A. bipunctata* larvae fed eggs of *C. s. brucki* survived, and none survived when fed eggs of *H. axyridis* ($\chi^2 = 40.2$, d.f. = 2, $P < 0.001$). Survival of *H. axyridis* larvae fed eggs of *A. bipunctata* and *C. s. brucki* was 0.35 and 0.85 times that when fed eggs of their own species ($\chi^2 = 22.5$, d.f. = 2, $P < 0.001$). No larvae of *C. s. brucki* survived when fed eggs of *H. axyridis* ($\chi^2 = 59.0$, d.f. = 2, $P < 0.001$), but all survived that were fed eggs of *A. bipunctata*. Therefore, for this species, the average duration of the first instar was also compared using the Mann–Whitney *U*-test. The average duration of development of first-instar larvae of *C. s. brucki* fed conspecific eggs was 3.1 ± 0.1 days ($n = 20$) eggs, and was prolonged significantly to 3.5 ± 0.1 days ($n = 20$), when fed *A. bipunctata* eggs ($U = 91.5$, $P < 0.001$).

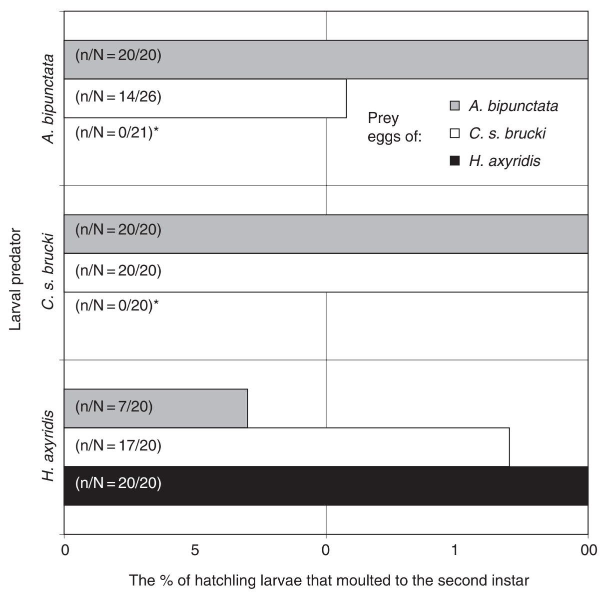

Figure 1 Percentages of hatchling larvae of *Harmonia axyridis*, *Coccinella septempunctata brucki* and *Adalia bipunctata* that moulted to the second instar when fed the eggs of their own or other species. *n*/*N* indicates the number of larvae that moulted to the second instar/number tested.

To examine further this chemical protection, the reluctance of larvae to eat the eggs of other species was determined. The average number of eggs consumed by first-instar larvae when fed eggs of their own species and other species is given in Fig. 2, and the results were compared using a Kruskal–Wallis test. The first-instar larvae of *A. bipunctata* consumed the eggs of *C. s. brucki* and *H. axyridis* at a third of the rate they consumed eggs of their own species ($\chi^2 = 35.8$, d.f. = 2, $P < 0.001$). The consumption of eggs by first-instar larvae of *C. s. brucki* also varied significantly ($\chi^2 = 38.6$, d.f. = 2, $P < 0.001$), those of *H. axyridis* were consumed at a third of the rate, and those of *A. bipunctata* at 1.2 times the rate they consumed eggs of their own specie. However, the eggs of *A. bipunctata* are smaller (0.6 times) than these of *C. s. brucki* (Sato, 2001). Therefore, it is likely that the higher rate of consumption of eggs of *A. bipunctata* by *C. s. brucki* larvae is because of the relative size of the eggs of the two species. First-instar larvae of *H. axyridis* consumed the eggs of *A. bipunctata* and *C. s. brucki* 0.6 and 0.8 times at the rate at which it consumed eggs of its own species ($\chi^2 = 13.5$, d.f. = 2, $P < 0.001$).

Discussion

When two predatious species co-occur in the same habitat, they are likely to be protected from intraguild predation in some way. In aphidophagous guilds, the larger species are likely to be intraguild predators and the smaller species intraguild prey (Sengonca & Frings, 1985; Lucas *et al.*, 1998; Phoofolo & Obrycki, 1998; Hindayana *et al.*, 2001). Accordingly, in terms of body size, *C. septempunctata* is unlikely to be the intraguild prey of *A. bipunctata* (i.e. it is likely the large species is physically protected from intraguild predation by the small species). In addition, small species may not be intraguild prey of large species, because they are more protected chemically against predation than *vice versa* (Agarwala & Dixon, 1992; Hemptinne *et al.*, 2000). That is, species of ladybirds that frequently co-occur may be protected from intraguild predation in some way.

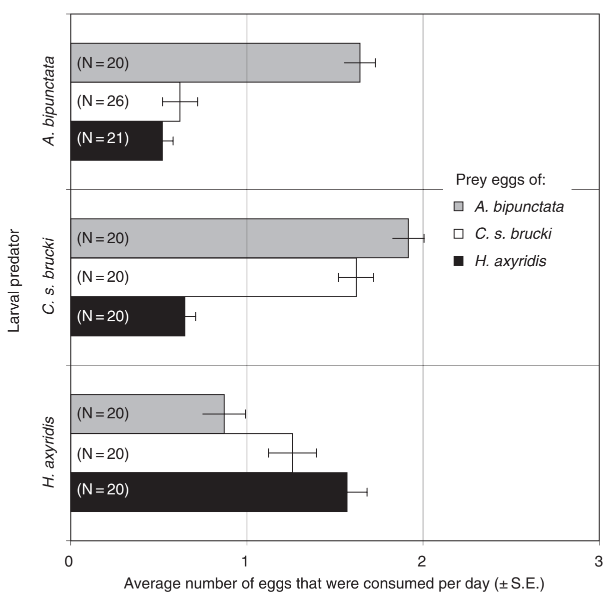

Figure 2 Average number of eggs consumed during first instar when fed the eggs of their own or other species. *N* indicates the number of hatchling larvae tested.

Harmonia axyridis and *C. s. brucki* commonly co-occur in the same habitat in spring (Takahashi & Naito, 1984; Takahashi, 1989; Yasuda & Shinya, 1997; Sato, 2001). Although all developmental stages of *H. axyridis* and *C. s. brucki* are similar in size (Sato, personal observation), these species differ in time of oviposition; *C. s. brucki* starts ovipositing earlier than *H. axyridis* (Takahashi & Naito, 1984; Takahashi, 1989; Yasuda & Shinya, 1997; Sato, 2001). Consequently, the development of *H. axyridis* is likely to lag behind that of *C. s. brucki*. Because large body size is also likely to be a protection against intraguild predation (Sengonca & Frings, 1985; Lucas *et al.*, 1998; Phoofolo & Obrycki, 1998; Hindayana *et al.*, 2001), early oviposition by *C. s. brucki* reduces the likelihood of this species being eaten by *H. axyridis*. In addition, *H. axyridis* was strongly protected chemically from predation by *C. s. brucki,* but not the reverse. Therefore, in the field, although *H. axyridis* is likely to be physically vulnerable, it is strongly chemically protected against predation by *C. s. brucki*. In this ladybird guild, both *H. axyridis* and *C. s. brucki* appear to be protected to some extent from intraguild predation by one another. In addition, Sato (2001) also demonstrates that emigration by larvae of *C. s. brucki* is also a way of avoiding intraguild predation by *H. axyridis*.

If species generally are protected from intraguild predation by co-occurring species, then an invasive species may need to be protected from the intraguild predation it is likely to be exposed to when attempting to invade an aphidophagous guild. For example, *H. axyridis* has successfully invaded several habitats in North America (Day *et al.*, 1994; LaMana & Miller, 1996; Brown & Miller, 1998; Colunga-Garcia & Gage, 1998; McCorquodale, 1998). Several studies report that larvae of *H. axyridis* can complete their development or survive after feeding on other species of ladybird or aphidophagous predator in North America, whereas none of them survive after eating *H. axyridis* (Cottrell & Yeargan, 1998; Phoofolo & Obrycki, 1998). *H. axyridis* is well protected chemically from predation by American species of aphidophaga, and this chemical protection may have been important for the establishment of this invasive species. Accordingly, if *A. bipunctata* is to successfully invade the aphidophagous guild in Japan (Sakuratani, 1994), it needs to be well protected against the intraguild predation it will encounter.

However, this study indicates that *A. bipunctata* is not well protected chemically from predation by *C. s. brucki* and *H. axyridis*. In addition, it is smaller than either of these species. Consequently, *A. bipunctata* may not become abundant in Japan. In conclusion, some ladybirds are well defended against intraguild predation, which is suggested to be an important force structuring ladybird guilds (Yasuda & Shinya, 1997; Kajita *et al.*, 2000) and the interactions between species (Agarwala & Dixon, 1992; Hemptinne *et al.*, 2000). If this is generally true, then the relative defenses of ladybird species against intraguild predation are likely to be useful in predicting the impact that introduced ladybird species may have on the structure of native ladybird guilds.

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