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Effects of indigenous ladybird species (Coleoptera: Coccinellidae) on the survival of an exotic species in relation to prey abundance

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Abstract
Interspecific relationships between indigenous ladybird species, *Coccinella septempunctata* L. and *Harmonia axyridis* Pallas, and an exotic species, *Adalia bipunctata* (L.), were assessed in relation to prey abundance. The nature and relative strengths of interactions between indigenous and exotic ladybird species differed in relation to prey availability and species involved. Under conditions of high prey abundance, the negative effect of interactions was limited to slower larval development of *A. bipunctata* in the presence of *H. axyridis* larvae. Under conditions of limited food availability, intraguild predation often occurred and *C. septempunctata* and *H. axyridis* were intraguild predators and *A. bipunctata* was intraguild prey. *H. axyridis* larvae was a stronger intraguild predator of *A. bipunctata* than *C. septempunctata* larvae. Possible causes for limited habitat of *A. bipunctata* after invasion into Japan, and the decrease in abundance of native populations of *A. bipunctata* in the U.S.A. after introduction of *C. septempunctata* and *H. axyridis* are discussed in relation to interactions of *A. bipunctata* with *C. septempunctata* and *H. axyridis*.

Key words: Biological control, Coccinellidae, cannibalism, competition, intraguild predation

INTRODUCTION

In view of an increasing awareness of sustainable agriculture in recent times, much attention is being paid to utilize indigenous and/or exotic predators in the control of pest insects instead of spraying large amount of pesticides. The famous example of success in biological control of the cottony cushion scale, *Icerya perchasi* Maskell, by a predacious coccinellid, *Rodolia cardinalis* (Mulsant), has led to a spurt in determining the potency of predatory ladybird species and their use against a number of aphids and coccids (e.g., Van Driesche and Bellows, 1996). However, most attempts in this direction have been unsuccessful (e.g., Obrycki and Kring, 1998).

In the U.S.A., many species of predatory ladybirds have been introduced in order to control pest insects (Obrycki and Kring, 1998). Some of the introduced species have influenced the structure of the prevailing ladybird assemblages. For example, introduced *Coccinella septempunctata* L. resulted in a decrease in the incidences of the two small-sized species, *Adalia bipunctata* (L.) and *C. transversoguttata richardsoni* Brown (Elliott et al., 1996), and the subsequent invasion by *Harmonia axyridis* Pallas led this species to become dominant by replacing *C. septempunctata* (Brown and Miller, 1998). In Japan, on the other hand, adults of *A. bipunctata* were first reported from Osaka (Sakuratani, 1994). Since then, there has been no other report indicating the expanded distribution of this species. The limited habitat of this exotic species in Japan might be attributable to its strong interactions with indigenous ladybird species.

There are a number of studies on intra and interspecific relationships between predatory ladybirds, and the nature and relative strengths of these interactions change with regard to food levels and the species involved (Takahashi, 1989; Evans, 1991; Agarwala and Dixon, 1992; Yasuda and Shinya, 1997; Obrycki et al., 1998a, b; Agarwala and Bardhanroy, 1999; Yasuda and Ohnuma, 1999). However, with the exception of one by Obrycki et al. (1998a, b), these studies focused mainly on the relationships between indigenous ladybird species. Thus, the mechanisms responsible for the limited habitat of *A. bipunctata* in Japan, and the dominance of the introduced species over the indigenous species in the U.S.A. are still unknown. More

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recently, there have been some studies which show the consequence of impacts of multiple predators on prey (Sih et al., 1998). However, there is clearly a lack of information about the impacts of introduced or exotic species of ladybirds on the guild of native ladybirds through a reduction in prey abundance, particularly in the context of Japan. Studies on interactions between ladybird species would contribute to our understanding of not only the methods of effective biological control for pest insects by multiple predators but also the mechanisms responsible for structuring ladybird assemblages.

In this study, the impacts of indigenous ladybird species, *C. septempunctata* and *H. axyridis*, were assessed on the larval survival of the exotic species, *A. bipunctata*, in relation to prey abundance. The influence of these interactions in the shaping of guilds of ladybird species not only in Japan but in the U.S.A., as well, is also discussed.

MATERIALS AND METHODS

The cowpea aphid, *Aphis craccivora* Koch, was collected from bean plants, *Vicia faba* L., and adults of the ladybirds, *C. septempunctata* and *H. axyridis*, were from hibiscus trees, *Hibiscus syriacus* L., or bean plants in the field at Yamagata University. Eggs of *A. bipunctata* were obtained from the University of East Anglia, Norwich, England and these were used successfully in raising a culture of larvae and adults in the laboratory. These ladybirds were maintained on cowpea aphids in plastic containers (15 cm in diameter and 9 cm in height) and the aphids were reared on bean plants. Eggs laid by the females were collected daily. Each egg batch was put individually into a 9 cm Petri dish and the larvae that hatched, were reared on cowpea aphids. The experiments and rearings of ladybirds and aphids in this study were carried out at a constant temperature (22±1°C) and photoperiod (L16:D8) in the laboratory.

Experiment 1: Interaction between exotic and indigenous ladybirds on high prey abundance. The following treatments were carried out in plastic containers (12 cm in diameter, 4.5 cm in height) that included an excess of mixed instars of aphids on two pieces of 5 cm long apical parts of bean plants: (1) four second stadium larvae of *A. bipunctata*; (2) two second stadium larvae of *A. bipunctata*+two second stadium larvae of *C. septempunctata*; and (3) two second stadium larvae of *A. bipunctata*+two second stadium larvae of *H. axyridis*. The pieces of bean plants with aphids were replaced daily and the containers were changed every three days. There was no mortality in the development of *C. septempunctata* and *H. axyridis* during this experiment. However, there was mortality of larvae of *A. bipunctata*. Therefore, results from all treatments in blocks where larval mortality of *A. bipunctata* was observed were eliminated from further analysis in terms of calculation for developmental time and weight gain. Each treatment was replicated 30 times except the treatment with *H. axyridis* which was replicated 10 times.

Although observations were made once a day until all the ladybirds were dead or had developed into adults, we observed the larvae as often as possible to detect cannibalism or intraguild predation (IGP). The number of living ladybirds, and whether or not they had moulted, were recorded at each observation. In the treatment involving a single species, the absence of ladybird larvae or the presence of parts of a ladybird carcass indicated cannibalism, while in treatments involving mixed species it indicated either cannibalism or IGP. A shrunken carcass of a ladybird was considered as death due to non-feeding.

Experiment 2: Interaction between exotic and indigenous ladybirds on limited prey abundance. In order to understand the effects of a limited food supply on intra and interspecific interactions, five treatments were done in 9 cm Petri dishes in the presence or absence of 50 adult aphids: (1) two fourth stadium larvae of *A. bipunctata* with aphids; (2) two fourth stadium larvae of *H. axyridis* with aphids; (3) two fourth stadium larvae of *C. septempunctata* with aphids; (4) a fourth stadium larva of *A. bipunctata*+a fourth stadium larva of *H. axyridis* with aphids; (5) a fourth stadium larva of *A. bipunctata*+a fourth stadium larva of *C. septempunctata* with aphids. Five other treatments with the same combinations of ladybird larvae but without aphids were also done. Observations were made at 12 and 24 h after the start of the experiment and the incidence of cannibalism or IGP was recorded. Each treatment was replicated 30 times.

The larvae used in the experiments were at 12 h

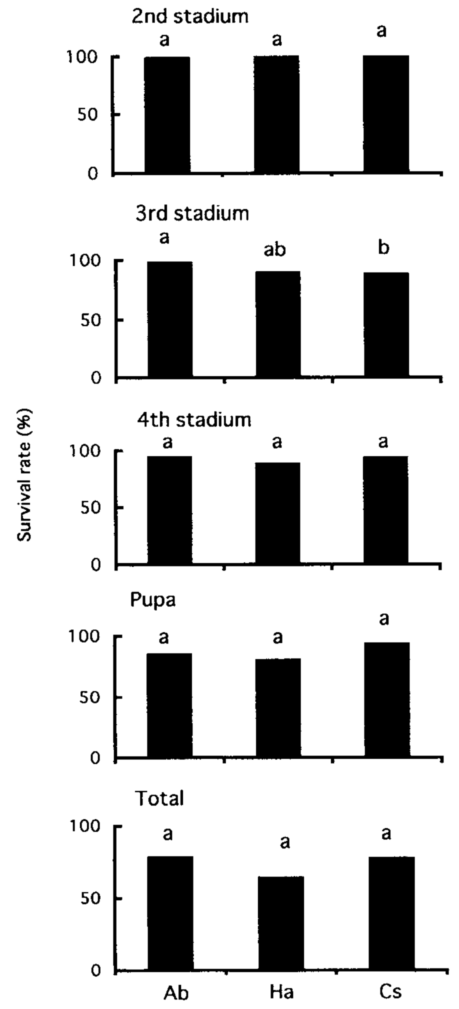

Fig. 1. Survival rate of *A. bipunctata* (Ab) at each developmental stage, when reared with conspecific or heterospecific larvae on high prey abundance. Ha and Cs indicate *H. axyridis* and *C. septempunctata*, respectively. Bars with the same letter are not significantly different (χ^2 test, $p>0.05$).

Table 1. Causes of mortality of *A. bipunctata* with conspecific or heterospecific larvae

	A. bipunctata		
	Alone	With Ha[b]	With Cs[b]
Survivors	95 (79.2)[a]	13 (65.0)	47 (78.3)
No. of individuals that died	25 (20.8)	7 (35.0)	13 (21.7)
Cannibalism	3 (2.5)	0 (0)	0 (0)
Predation	—	2 (10.0)	1 (1.7)
Failure in moulting	3 (2.5)	2 (10.0)	7 (11.7)
Failure in adult emergence	16 (13.3)	3 (15.0)	3 (5.0)
Non-feeding	3 (2.5)	0 (0)	2 (3.3)

[a] Figures in parenthesis show percentage of total individuals tested.

[b] Ha and Cs indicate *H. axyridis* and *C. septempunctata*, respectively.

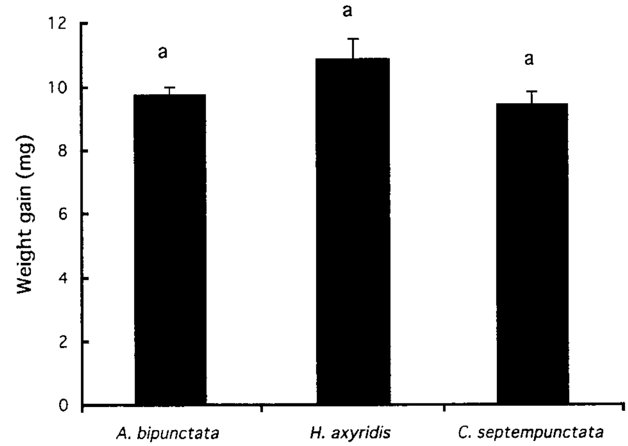

Fig. 2. Weight gain (mg) of *A. bipunctata* when reared with conspecific or heterospecific larvae on high prey abundance. Bars with the same letter are not significantly different (ANOVA, $p>0.05$).

after moulting. The data were analyzed using ANOVA and the survival rate was tested by χ^2.

RESULTS

Experiment 1: Interaction between exotic and indigenous ladybirds on high prey abundance

There was no significant difference in the survival rates of *A. bipunctata* larvae based on whether they were reared with heterospecific larvae or conspecific larvae except for the effect of *C. septempunctata* on the survival of *A. bipunctata* during the third stadium ($p>0.05$; Fig. 1). It is interesting to note that the larvae of *C. septempunctata* and *H. axyridis* ate *A. bipunctata* larvae in high prey abundance (Table 1). In terms of percentage of death due to failures in moulting and in adult emergence, 25% and 16.7% mortalities were recorded in treatments with *H. axyridis* and *C. septempunctata*, respectively, and 15.8% with conspecifics. However, there were no significant differences in mortality between treatments with conspecifics and with heterospecifics (with *H. axyridis*; $\chi^2=0.06$, $p>0.05$; with *C. septempunctata*, $\chi^2=0.004$, $p>0.05$).

Weight gained by *A. bipunctata* larvae during development in each treatment is shown in Fig. 2. There was no significant difference in the weight gained by the larvae of *A. bipunctata* between the treatments, whether with conspecific larvae or with heterospecific larvae ($p > 0.05$).

The developmental time of the surviving larvae of *A. bipunctata* in the treatment with conspecifics was significantly shorter than those with *H. axyridis* ($p < 0.05$), but it was not significantly different from those with *C. septempunctata* ($p > 0.05$; Fig. 3).

Experiment 2: Interaction between exotic and indigenous ladybirds on limited prey abundance

Survival rates of *A. bipunctata* larvae in treatment with conspecific or heterospecific larvae are shown in Fig. 4. Mortality factors were cannibalism or predation (Table 2). In treatments with 50 adult aphids at 12 h, there was no mortality of *A. bipunctata* larvae in treatments with conspecifics or *C. septempunctata*. However, significant mortalities of *A. bipunctata* occurred in interactions with *H. axyridis*. After 24 h, a significantly larger number of *A. bipunctata* larvae were eaten in interactions with *H. axyridis* larvae than in interactions with *C. septempunctata* larvae.

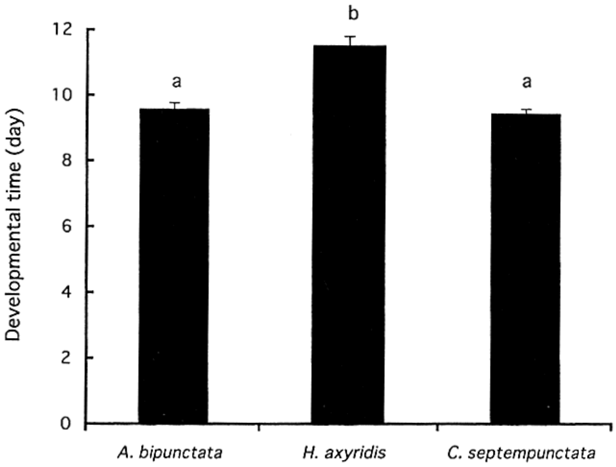

Fig. 3. Developmental time of *A. bipunctata* when reared with conspecific or heterospecific larvae on high prey abundance. Bars with different letters are significantly different (Scheffé's test, $p > 0.05$).

In treatments without aphids, mortality of *A. bipunctata* occurred due to cannibalism or IGP (Table 2). Mortality was low after 12 h but increased after 24 h. The effect of cannibalism or IGP was similar after 24 h, but a significantly higher mortality of *A. bipunctata* larvae was caused by IGP of *H. axyridis* larvae ($p < 0.05$).

There was no predation of *H. axyridis* or *C. septempunctata* larvae by *A. bipunctata* and there were no negative effects of *A. bipunctata* on the mortality of the two species (Table 2).

DISCUSSION

The nature and relative strengths of the interactions between indigenous and exotic ladybird species differed in relation to prey abundance and species involved. Under conditions of high prey abundance, the effects of indigenous species on larval performance of *A. bipunctata* was limited to a negative influence of *H. axyridis* larvae on the larval development of *A. bipunctata*. Under conditions of limited food supply, however, IGP occurred, and *C. septempunctata* and *H. axyridis*

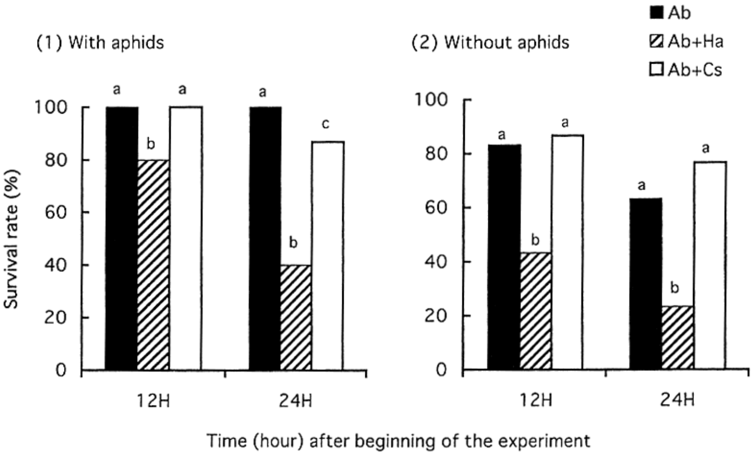

Fig. 4. Survival rate of *A. bipunctata* (Ab) when reared with a conspecific or heterospecific larva on limited prey abundance with or without aphids. Ha and Cs indicate *H. axyridis* and *C. septempunctata*, respectively. Bars with the same letter are not significantly different (χ^2 test, $p > 0.05$).

Table 2. Causes of mortality of *A. bipunctata*, *H. axyridis*, and *C. septempunctata* with conspecific or heterospecific larvae after 24 h

	A. bipunctata (Ab)			*H. axyridis* (Ha)		*C. septempunctata* (Cs)	
	Alone	With Ha	With Cs	Alone	With Ab	Alone	With Ab
(1) With aphids							
Survivors	60 (100)[a]	12 (40.0)	26 (86.7)	56 (93.3)	30 (100)	60 (100)	30 (100)
No. of individuals that died	0 (0)	18 (60.0)	4 (13.3)	4 (6.7)	0 (0)	0 (0)	0 (0)
Cannibalism	0 (0)	—	—	4 (6.7)	—	0 (0)	—
Predation	—	18 (60.0)	4 (13.3)	—	0 (0)	—	0 (0)
(2) Without aphids							
Survivors	38 (63.3)	7 (23.3)	23 (76.7)	39 (65.0)	30 (100)	52 (86.7)	30 (100)
No. of individuals that died	22 (36.7)	23 (76.7)	7 (23.3)	21 (35.0)	0 (0)	8 (13.3)	0 (0)
Cannibalism	22 (36.7)	—	—	21 (35.0)	—	8 (13.3)	—
Predation	—	23 (76.7)	7 (23.3)	—	0 (0)	—	0 (0)

[a] Figures in parenthesis show percentage of total individuals tested.

were intraguild predators and *A. bipunctata* was intraguild prey.

The nature and relative strengths of intra and interspecific relationships were found to be associated with prey availability (Obrycki et al., 1998a); no interspecific interactions were observed between larvae of *C. septempunctata* and *C. maculata* (DeGeer) at a high prey density, but *C. septempunctata* caused negative effects on larval performance of *C. maculata* under conditions of limited food availability. In another study, Evans (1991) showed that interspecific competition among four ladybird species did not differ from intraspecific competition in terms of larval performance and prey consumption. Obrycki et al. (1998a) mentioned the consequence of prey availability on the incidence of interactions as shown in this study. Therefore, the lack of a difference between intra and interspecific interactions among these larvae in the results of Evans (1991) is possibly attributable to high food availability. In this study, however, developmental time of *A. bipunctata* was prolonged in the treatment with *H. axyridis* even under high food availability. This tendency is of interest, but the mechanism is not yet understood. Intraguild prey species may change their foraging behaviour in the presence of intraguild predators (e.g., Johansson, 1993a, b; Schmitz et al., 1997) and this may influence the development of intraguild prey. This needs to be investigated in the context of the interactive relationship between *A. bipunctata* and *H. axyridis*. Obrycki et al. (1998a) suggested that competition and IGP were two possible mechanisms between coccinellid larvae, however, there is no evidence to show the relative importance of these two interactions. Our results showed that IGP occurred in relation to prey availability, and between *H. axyridis* and *C. septempunctata* larvae: the former was a stronger intraguild predator of *A. bipunctata* larvae. In terms of food habit, *H. axyridis* is a polyphagous species (Hodek and Honek, 1988, 1996) and its larvae are more polyphagous than those of *C. septempunctata* (Lucas et al., 1997; Yasuda and Ohnuma, 1999). Furthermore, *H. axyridis* is a more aggressive species than *C. septempunctata* (Yasuda, unpubl.). These differences in food habit and aggressive behaviour between the two indigenous species of ladybirds might have caused the difference in the incidence of IGP of *A. bipunctata*.

After *C. septempunctata* was introduced into the U.S.A., this species became a dominant species, and the abundance of two small-sized ladybird species including *A. bipunctata* was significantly reduced (Elliot et al., 1996). The mechanisms of replacement are not well known, however, as shown in the present study, IGP by *C. septempunctata* may be one of the causes of reduced abundance of *A. bipunctata*, especially under limited prey availability. Cannibalism is well known in ladybirds and in other predatory arthropods (e.g. Elgar and Crespi, 1992; Hodek and Honek, 1996), and it is considered to influence the population regulation of several species of predatory arthropods

(Van Buskirk, 1989; Hopper et al., 1996; Wagner and Wise, 1996). In addition, our results showed that *A. bipunctata* larvae often cannibalized when faced with food scarcity. Large-sized coccinellid species usually take advantage of small-sized ladybird species in terms of food consumption, and this could result in asymmetrical interactions between the two species (Obrycki et al., 1998a). Thus, the intensity of IGP by *C. septempunctata* and/or cannibalism might increase since a large amount of prey consumption by introduced large-sized *C. septempunctata* leads to a decrease in prey abundance.

In light of the above, it is likely that the invasion of *A. bipunctata* is checked in Japan due to the negative effects of interactions with the indigenous species, in particular, IGP by *H. axyridis*, as shown in present study. This could explain why *A. bipunctata* has not been reported from new areas since its invasion in the port town of Osaka more than six years ago (Sakuratani, 1994 and personal communication). Additionally, *A. bipunctata* prefers trees as its habitat which is also the preferable habitat of *H. axyridis*. On hibiscus trees, the fact that IGP by *H. axyridis* on other ladybird species is the most important force in structuring the ladybird assemblages might support this scenario (Sato, 1997; Yasuda and Shinya, 1997).

IGP and cannibalism are considered as determinants of population dynamics and structure of biological communities (Polis et al., 1989; Elgar and Crespi, 1992; Polis and Holt, 1992; Holt and Polis, 1997). This has been well documented through a number of studies in aphidophagous assemblages (Takahashi, 1989; Agarwala and Dixon, 1992; Rosenheim et al., 1993, 1995; Ferguson and Stiling, 1996; Cisneros and Rosenheim, 1997; Dinter, 1998; Lucas et al., 1998; Phoofolo and Obrycki, 1998; Yasuda and Ohnuma, 1999; Yasuda and Kimura, 2000). Food availability for aphidophagous insects is often uncertain as the number of aphids in a patch changes rapidly in time and space (e.g. Yasuda and Shinya, 1997; Dixon, 1998; Osawa, 2000). As a result, not only ladybirds but also other aphidophagous arthropods would often face food scarcity or starvation. The findings that adult ladybirds collected from fields were smaller than the ones reared in the laboratory suggest that larvae of ladybirds often lived in habitats with poor food availability (Obrycki et al., 1998a). In such an environment, though competition and predation between aphidophagous insects are both important interactions, the latter might be a limiting factor in structuring the assembly of aphidophagous insects.

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