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Effect of cannibalism and predation on the larval performance of two ladybird beetles

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Abstract

The relative impact of cannibalism and predation on the development and survival of fourth instar larvae was assessed in two species of aphidophagous ladybird beetles, *Coccinella septempunctata* and *Harmonia axyridis*. The effect of eating aphids, conspecific larvae or heterospecific larvae on larval performance differed in the two species: aphids were the best food for *C. septempunctata* and survival of *C. septempunctata* larvae was significantly lower when offered heterospecific larvae rather than conspecific larvae or aphids as food, indicating that *H. axyridis* larvae were not suitable food for *C. septempunctata*. However, as the different foods did not affect the larval performance of *H. axyridis*, this species appears to be more polyphagous. Both intraguild predation by the aggressive larvae of *H. axyridis* and the polyphagous food habit of this species may account for its dominance in ladybird assemblages and its displacing other ladybird beetles in several places in the world.

Introduction

In biological communities complex trophic interactions and more recently cannibalism and intraguild predation (IGP) are seen as important determinants of population dynamics and community structure (Polis et al., 1989; Polis & Holt, 1992). For example, in the wolf spider, *Schizocosa ocreata*, cannibalism acts as a strong density dependent mortality factor which seems to regulate the population density of the spider (Wagner & Wise, 1996). In addition, in larval odonate communities, cannibalism and IGP are often observed and sometimes are important factors structuring these communities (Spence & Carcamo, 1991; Johansson, 1993; Fincke, 1994; Wissinger et al., 1996). Therefore, in order to understand how arthropod predatory guilds are structured it is necessary to determine the effect of these factors on predators.

Predatory ladybird beetles can mainly be categorized as either aphidophagous or coccidophagous depending on the nature of their prey. The developmental times of these two groups of ladybirds are related to their prey species (Dixon et al., 1997). In the case of aphidophagous ladybirds, larval performance is influenced by the quality of aphids (Blackman, 1967; Hukushima & Kamei, 1970; Hamalainen & Markkula, 1972; Pasteels, 1978; Hodek & Honek, 1996). In addition to this, a number of researchers have revealed the effects of egg cannibalism and egg predation by larvae of several ladybird beetle species on their survival and/or development (Koide, 1962; Warren & Tadic, 1967; Kawai, 1978; Agarwala, 1991; Agarwala & Dixon, 1992). Furthermore, the ladybirds contain species-specific toxins which are differentially toxic to animals (Pasteels et al., 1973; Marples et al., 1989; Agarwala & Bhattacharya, 1995). It is known that cannibalism and IGP occur in aphidophagous ladybird beetles and varies in intensity between species (Takahashi, 1989; Agarwala & Dixon, 1992; Yasuda & Shinya, 1997). Therefore, cannibalism and predation in ladybird beetles may affect their development and survival differently. However, there are few studies on the effects of conspecific and/or heterospecific interactions between ladybird larvae on their performance.

Table 1. Mortality of the fourth instar larvae of two species of ladybird beetles fed one of three different kinds of prey

Predator	Prey	No. of individuals that died	Mortality due to		Survival rate (%)	*n*
			Starvation	Unknown		
H. axyridis (Ha)	Aphid	1	0	1	92.9a	14
	Ha	2	2	0	87.5a	16
	Ca	1	0	1	93.3a	15
C. septempunctata (Cs)	Aphid	1	0	1	93.3a	15
	Ha	13	13	0	18.8b	16
	Cs	2	1	1	84.6a	13

Numbers with same letter are not significantly different in the survival rate between prey species (χ^2-test, $P > 0.05$).

In the farm at Yamagata University, in northern Japan, five species of aphidophagous ladybird beetles coexist on *Hibiscus syridis,* which is the primary host of the cotton aphid, *Aphis gossypii*. Of the ladybird beetles, *Coccinella septempunctata* and *Harmonia axyridis*, are the most abundant species. Although it is known that cannibalism and IGP occur between these two species when prey is scarce, and that IGP is asymmetrical (Yasuda & Shinya, 1997), little is known about the effects of these interactions on larval survival and development. In this study, we assess the relative impacts of cannibalism and predation on the performance of the larvae of two ladybird species, especially during the fourth instar, which is the most voracious stage.

Table 2. Number ($\overline{x} \pm$ SE) of conspecific and heterospecific larvae eaten by the two species of ladybird beetles

Predator	Prey	Number eaten	n^3
H. axyridis: developed[1] (Ha)	Ha	5.92 ± 0.71	14
	Cs	5.28 ± 0.38	14
H. axyridis: starved[2]	Ha	2	2
	Cs	–	0
C. septempunctata: developed (Cs)	Ha	6.33 ± 0.88	3
	Cs	5.00 ± 0.42	11
C. septempunctata: starved	Ha	1.25 ± 0.30	13
	Cs	0	1

[1]'Developed' indicates that the fourth instar larvae pupated.
[2]'Starved' indicates that the fourth instar larvae died of starvation.
[3]Deaths due to unknown causes were not included.

Materials and methods

Eggs of the two ladybird species were collected from trees of *H. syridis* in Tsuruoka (38°43′ N, 139°49′ E) and were kept in 9 cm Petri dishes. The larvae that hatched from these eggs were reared on cotton aphids.

A less than 12 h old fourth instar larva of *C. septempunctata* or *H. axyridis* was placed in a Petri dish with a conspecific or heterospecific fourth instar larva as food. As preliminary experiments showed that intact *H. axyridis* larvae offered as prey attacked and killed *C. septempunctata* larvae, the legs of larvae supplied as food were removed.

Observations were made at 08:00 and 19:00 each day until the larvae died or developed into adults and the incidence of predation and/or pupation were recorded. The cause of mortality was recorded as starvation or unknown. The presence of a shrunken carcass indicated starvation and a more normal sized carcass was considered as death due to an unknown factor. In order to compare the larval performance when fed aphids or larvae, fourth instar larvae of *C. septempunctata* and *H. axyridis* were reared individually with either 50 adult cotton aphids on a leaf of *H. syridis* or a ladybird larva in Petri dishes. The aphids were replaced every 24 h and the ladybird larva every 12 h. The weight of the ladybirds was measured to the nearest 0.01 mg at the beginning of the experiment and on the day following pupation. Weight gain during the fourth instar was calculated as follows; Weight gain = Weight of pupa − Weight of fourth instar larvae at the beginning of the experiment.

All experiments, including rearing of larvae, were done in an incubator at a constant temperature of 22 ± 1.0 °C and a photoperiod of L16:D8. Data were analysed using ANOVA and mean differences separated using Tukey's HSD multiple comparison test. The survival rate was tested by χ^2.

Results

Survival. Survival of *C. septempunctata* larvae was significantly lower when given heterospecific larvae as food than when given conspecific larvae or aphids (P<0.05; Table 1). The larvae offered heterospecific larvae mostly starved to death as 81.3% of the larvae did not eat the legless *H. axyridis* larvae. In contrast, there was no significant difference in the mortality of *H. axyridis* larvae fed the three preys (P > 0.05) and most larvae pupated. When *H. axyridis* larvae were offered conspecific larvae as food, 12.5% of them died of starvation. All pupae of *H. axyridis* developed into adults, irrespective of the nature of the prey eaten. However, in *C. septempunctata* only three pupae out of 16 larvae developed when they were fed *H. axyridis* larvae and eleven out of 13 larvae developed when fed *C. septempunctata* larvae. Of these, one reared on conspecific larvae and one on heterospecific larvae failed to emerge.

Food consumption. The larvae of both ladybird beetle species, which pupated, ate five to six conspecific or heterospecific larvae during the fourth instar (Table 2) and the number of individuals eaten by each species did not differ significantly (Kruskal–Wallis test; P > 0.05). However, in both species the larvae that died each ate less than two larvae.

Weight gain. Weight gained by both species during the fourth instar when fed one of the three prey types is shown in Figure 1. Weight gain in *C. septempunctata* was higher when fed aphids than coccinellid larvae (P > 0.05), indicating that in terms of weight gain aphids were a very suitable food for *C. septempunctata*. The weight gain of *H. axyridis* larvae was independent of prey type (P > 0.05).

Developmental time. The fourth instar larvae of both species took approximately a week to pupate (Figure 2) and this was not affected by the nature of the prey supplied (P > 0.05).

Discussion

The effects of the different prey on larval performance differed between the two species: aphids were the best food for *C. septempunctata* and *H. axyridis* larvae the worst. As for *H. axyridis*, the different prey appeared equally suitable.

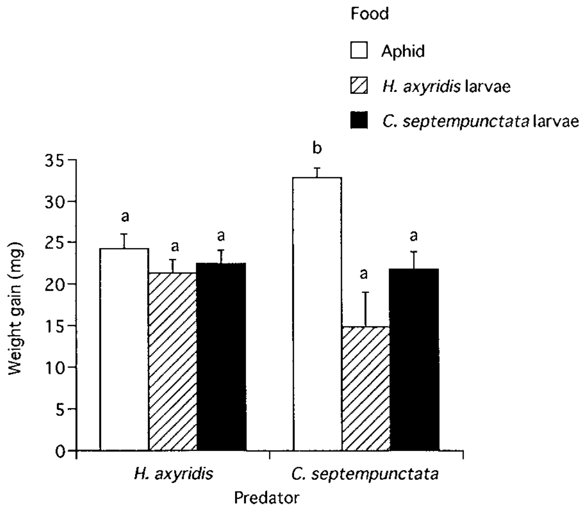

Figure 1. Weight gain (mg) of the fourth instar larvae of two species of ladybird beetles fed one of three different kinds of prey. Bars labeled with the same letter are not significantly different (Tukey–Kramer test, P > 0.05).

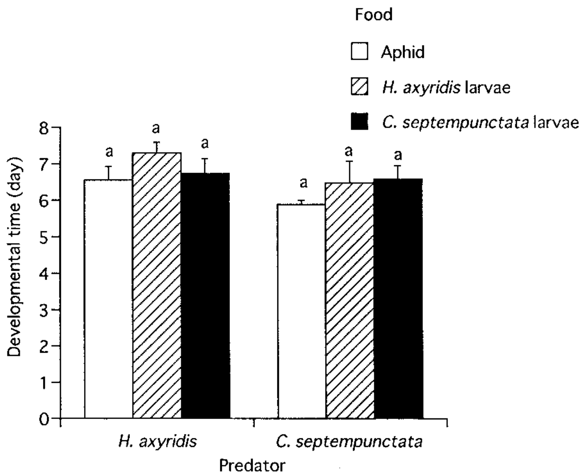

Figure 2. Developmental time of the fourth instar larvae of two species of ladybird beetles fed one of three different kinds of prey. Bars labeled with the same letter are not significantly different (ANOVA, P > 0.05).

The performance of the larvae of predatory ladybird beetles is often affected by the species of aphid they eat (Blackman, 1967; Hukushima & Kamei, 1970; Hamalainen & Markkula, 1972; Pasteels, 1978). The mortality of *H. axyridis* fed *Aphis craccivora* depends upon the species of plants the aphids fed on, which suggests that chemical substance in the food affected the survival of the ladybird (Hukusima & Kamei, 1970). Several species of ladybirds contain alkaloids which have a different structure and they are an effective defense against ants, *Myrmica rubra*, and quails, *Coturnix coturnix* (Pasteels et al., 1973). The nature and the effect of these alkaloids differ between ladybird beetles, e.g., *C. septempunctata*, but not *Adalia bipunctata*, is highly toxic for nestling blue tits, *Parus coeruleus* (Marples et al., 1989). In addition, egg cannibalism was often observed in a number of ladybird beetle species and eggs were nutritious for the larvae (Koide, 1962; Warren & Tadic, 1967; Kawai, 1978; Takahashi, 1987; Agarwala, 1991; Agarwala & Dixon, 1992) . The cannibalism is known to be beneficial when aphid density is low (Agarwala, 1991; Osawa, 1992a) and eggs are better food than aphids for young larvae in terms of larval growth and survival (Kawai, 1978; Agarwala & Dixon, 1992). Egg predation by larval ladybirds sometimes can affect their survival and the effect differs between species: *C. septempunctata* larvae tended to die after eating a few eggs of *A. bipunctata*, however, this was less likely when *A. bipunctata* larvae ate eggs of *C. septempunctata*. (Agarwala & Dixon, 1992). These findings indicate that the quality of prey is important for aphidophagous ladybirds, and predation might result in death. In the present study, when *H. axyridis* larvae were supplied as food to *C. septempunctata* larvae, 80% of them died. But, this was due to starvation and not the consequence of eating *H. axyridis* larvae. In the case of *H. axyridis* larvae, most pupated after eating both conspecific and heterospecific larvae. These results indicate that the toxin in the larvae of the two species does not appear to determine larval mortality in these species. However, eating conspecific larvae or heterospecific larvae may influence adult longevity and reproduction.

Aphidophagous ladybird beetles will eat conspecific and/or heterospecific eggs, larvae, and pupae depending on the availability of aphid prey (Kawai, 1978; Mills, 1982; Osawa, 1989, 1992b; Takahashi, 1989; Agarwala & Dixon, 1992; Yasuda & Shinya, 1997) and the incidence of cannibalism and predation differs between species (Takahashi, 1987; Agarwala & Dixon, 1992; Yasuda & Shinya, 1997); *Coccinella* larvae ate more conspecific than heterospecific larvae, but *Adalia* larvae ate more heterospecific than conspecific larvae (Agarwala & Dixon, 1992). In terms of predation *H. axyridis* larvae often ate *C. septempunctata* larvae, but the reverse is rare (Yasuda & Shinya, 1997). *H. axyridis* is a polyphagous species (Hodek & Honek, 1988) and Lucas et al. (1997) have also shown that *H. axyridis* larvae are more polyphagous than those of *C. septempunctata*. The present study indicates that weight gain in *C. septempunctata* larvae was highest when fed aphids, but that food type had no affect on the larval performance of *H. axyridis*. Therefore, it seems that *C. septempunctata* is a more aphid-specific predator than *H. axyridis*.

The legs of the ‘prey individuals’ were cut off in order to prevent the ‘prey’ eating the ‘predator’ in this study. In preliminary experiments all the *C. septempunctata* larvae were killed by intact *H. axyridis* larvae, but no larvae of *H. axyridis* were eaten by *C. septempunctata* larvae. So, not only are *H. axyridis* larvae polyphagous they are also very voracious, whereas those of *C. septempunctata* are oligophagous and less aggressive.

The effect of an invading species on a native ladybird assemblage was studied on apple trees in eastern West Virginia for 8 years (Brown & Miller, 1998). After the invasion by *C. septempunctata* in 1983, the assemblage was dominated by *C. septempunctata*, and subsequent invasion of *H. axyridis* in 1994 resulted in this species replacing *C. septempunctata* as the dominant species. This replacement of *C. septempunctata* by *H. axyridis* has also been reported in agricultural and natural ecosystems in midwestern USA (Horn, 1996). However, the mechanism of the replacement has not been known. Our findings on the aggressive behaviour of *H. axyridis* provide one of the possible explanations. The relationship between *C. septempunctata* and *H. axyridis* in northern Japan was studied using life table analysis (Yasuda & Shinya, 1997). *H. axyridis* was the dominant species in 2 years and the mechanism was IGP by *H. axyridis* larvae on those of *C. septempunctata* after the aphid became scarce. Both IGP and the polyphagous habit of *H. axyridis* negatively affect the larval performance of *C. septempunctata* and contribute to the replacement of this species by *H. axyridis*.

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