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Effects of intra and interspecific interactions on the survival of two predatory ladybirds (Coleoptera: Coccinellidae) in relation to prey abundance

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Abstract
The relative effects of intra and interspecific interactions on the larval survival of two species of aphidophagous ladybirds, *Coccinella septempunctata brucki* and *Harmonia axyridis*, were assessed at two different prey abundances. In single species rearing, the number of larvae of both species decreased during the latter developmental stages, mainly due to cannibalism. When prey was abundant, the survival of both species improved; however, in mixed species rearing, the mortality of *C. septempunctata brucki* due to cannibalism or intraguild predation was higher than in single species rearing, whereas the mortality was lower in *H. axyridis*. Consequently, the survival of *C. septempunctata brucki* decreased while that of *H. axyridis* improved. In addition, in the 18 intraguild predation events observed, *H. axyridis* was always the intraguild predator and *C. septempunctata brucki* was its prey. Thus, when these two species co-exist in the field, *H. axyridis* is likely to be an important intraguild predator of *C. septempunctata brucki*. In addition, when prey is scarce, it is likely that cannibalism and intraguild predation become more important factors in the intra and interspecific relationships of these two species.

Key words: Cannibalism; guild structure; intraguild predation; intra and interspecific interaction; predatory ladybird

INTRODUCTION

Competition, predation, and disturbance are important in shaping communities (e.g. Menge and Sutherland, 1987; Begon et al., 1996). Intraguild predation is common among arthropods in agricultural (Rosenheim et al., 1993, 1995; Cisneros and Rosenheim, 1997) and natural ecosystems (Moran and Hurd, 1994; Snyder and Hurd, 1995); therefore, intraguild predation is thought to be an important factor affecting population dynamics and community structure in several taxa of predatory arthropods (Polis et al., 1989; Spence and Carcamo, 1991; Polis and Holt, 1992; Fincke, 1994; Wagner and Wise, 1996; Holt and Polis, 1997; Mizell, 2007; Montserrat et al., 2008).

Many species of predatory arthropods are attracted to sites where aphids are abundant (Sakuratani, 1977; Aalbersberg et al., 1988; Winder et al., 1994; Wyss, 1995; Nakashima and Akashi, 2005; Alhmedi et al., 2007). In these aphidophagous guilds, intraguild predation often occurs and its incidence depends on prey abundance and the developmental stages and species of the predator involved (Takahashi, 1989; Agarwala and Dixon, 1992; Rosenheim et al., 1993; Cisneros and Rosenheim, 1997; Dinter, 1998; Lucas et al., 1998; Obrycki et al., 1998; Phoofolo and Obrycki, 1998).

Of these aphidophagous arthropods, ladybirds are important, and because of their voracity and size they affect the survival of other aphidophagous insects (Lucas et al., 1998; Obrycki et al., 1998); however, the nature and relative strengths of intraguild predation on larval survival have not been quantified. Knowledge of the effect of these interactions on their performance throughout their larval development, when they coexist in the same habitat, is needed for a better understanding of

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their relative importance and role in shaping aphidophagous guilds.

In Japan, *Coccinella septempunctata brucki* Mulsant and *Harmonia axyridis* Pallas coexist in the same habitat, e.g., these two species co-occur on *Hibiscus syridis* Linne, the primary host of the cotton aphid, *Aphis gossypii* Glover at the farm of Yamagata University in northern Japan (Yasuda and Shinya, 1997). Cannibalism and intraguild predation between these two species are sometimes observed in the field when prey is scarce (Takahashi, 1989; Yasuda and Shinya, 1997), suggesting that intra and interspecific competition may also affect interactions between these two species. The aim of this study was to assess the nature and relative strengths of intra and interspecific interactions between the larvae of ladybirds *C. septempunctata brucki* and *H. axyridis* by determining the relative effects of competition and/or predation on larval survival of these two species when prey is scarce and abundant. The role of these interactions in determining guild structure in ladybirds is discussed.

MATERIALS AND METHODS

The cotton aphid, *A. gossypii*, and adults of ladybirds, *C. septempunctata brucki* and *H. axyridis*, were collected from hibiscus trees growing in a field at Yamagata University. Adult ladybirds were fed cotton aphids in plastic containers (15 cm in diameter and 9 cm in height) and eggs laid were collected every day. Each egg batch was placed individually in a Petri dish (9 cm in diameter) and 24–48 h after hatching, the larvae were used in experiments. The ladybirds were reared at a constant temperature (25±1°C) and photoperiod (16L8D) in a laboratory.

Each hibiscus tree, 60 cm in height, was planted individually in a standard plant pot, and three aluminum poles (76 cm in height) were inserted into the soil around the rim of the pot. Each tree was enclosed in a nylon screen bag, which was taped to the top of the pot. Each tree was infested with approximately 300 (low prey density) or 700 (high prey density) adult cotton aphids and subjected to one of the following treatments, each replicated three times: 10 first instar larvae of *C. septempunctata brucki* (1) or of *H. axyridis* (2), or five first instar larvae of each of these species (3). Treatments 1 and 2 are referred to as single species experiments and treatment 3 as a mixed species experiment. The numbers of aphids and ladybird larvae used in these experiments are within the range of numbers observed in the field (Sato, unpublished data).

The numbers of ladybird larvae and their instar was recorded daily until all ladybirds were dead or had developed into adults. To determine the cause of mortality, the larvae were observed as often as possible and any cannibalism or intraguild predation recorded. In the single species experiments, the disappearance of a larva or presence of parts of a carcass indicated cannibalism, while in the mixed species experiment it indicated either cannibalism or intraguild predation. A shrunken carcass indicated starvation. Death due to a cause other than cannibalism, intraguild predation or starvation was categorized as "other mortality"; that is, the cause of death of a ladybird larva was decided on the basis of the condition of its carcass. All experiments were carried out in a greenhouse. The mean daily temperature in the greenhouse during the experiments was 20–26°C. Because there were a few replicates and few larvae survived, the results for all replicates of each treatment were pooled. The results were compared using chi-squared tests.

RESULTS

The number of aphids present was not monitored during the present experiments; however, the developmental stages of larvae of both species when aphids became extinct appeared to depend on initial prey density; there were third and fourth instars, respectively, in the low and high prey density treatments in the following two experiments.

Single species experiment

In the low prey density treatment, the number of larvae of both species decreased, mainly over the period from the third instar to pupal stage, and none completed their development (Fig. 1-1a); however, in the high prey density treatment, more than 30% of the larvae of both species completed their development and emerged as adults (*C. septempunctata brucki*: $\chi^2=12.0$, d.f.$=1$, $p<0.0001$; *H. axyridis*: $\chi^2=18.3$, d.f.$=1$, $p<0.0001$) (Fig. 1-1b); that is, although the percentage survival of both species tended to decrease during the latter developmental stages, more survived at the

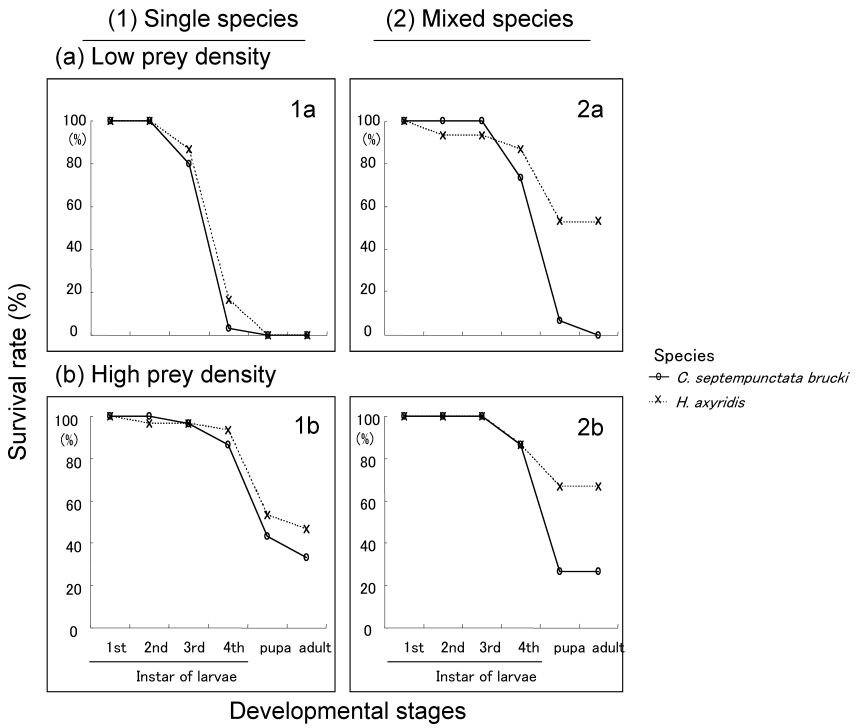

Fig. 1. Survival rate of two species of aphidophagous ladybirds, *C. septempunctata brucki* and *H. axyridis*, at each developmental stage when reared in single and mixed species treatments at two prey population densities.

higher prey density.

In the low prey density treatment, the percentage of larvae of *C. septempunctata brucki* that died due to cannibalism compared to other causes of mortality differed significantly ($\chi^2=18.3$, d.f.$=2$, $p<0.0001$) (Fig. 2-1a) with cannibalism accounting for 6 times more of the deaths than the other causes of mortality. Similarly, in *H. axyridis*, cannibalism accounted for most deaths, but the differences in mortality attributable to the different causes of death were not significant ($\chi^2=3.6$, d.f.$=2$, $p>0.05$). Consequently, cannibalism accounted for more deaths in *C. septempunctata brucki* than *H. axyridis* ($\chi^2=10.8$, d.f.$=1$, $p<0.001$); however, in the high prey density treatment, the percentages of deaths attributable to cannibalism were halved in both species compared with in the low prey density treatment (*C. septempunctata brucki*: $\chi^2=12.4$, $p<0.0001$; *H. axyridis*: $\chi^2=4.8$, $p<0.05$) (Fig. 2-1b); that is, in general, the main cause of mortality was cannibalism in both species, and this tended to decrease when prey was abundant.

Mixed species experiment

Similarly, in the mixed species experiment, at both prey densities, the numbers of larvae of both species tended to decrease during the latter developmental stages (Fig. 1-2a, 2b). In the low prey density treatment, no larvae of *C. septempunctata brucki* completed their development (Fig. 1-2a), whereas 53% of the larvae of *H. axyridis* reached the adult stage, which is significantly more than the 0% in the single species experiment ($\chi^2=19.5$, d.f.$=1$, $p<0.0001$) (Fig. 1-1a, 2a). In the high prey density treatment, the percentage of larvae of *H. axyridis* that reached the adult stage was significantly higher than in the single species experiment, but not significantly so ($\chi^2=0.6$, d.f.$=1$, $p>0.05$) (Fig. 1-1b, 2b). Twice the number of larvae of *H. axyridis* reached the adult stage than of *C. septempunctata brucki* ($\chi^2=4.8$, d.f.$=1$, $p<0.05$, Fig. 1-2b); that is, at both prey densities, the survival of *H. axyridis* was greatly increased if *C. septempunctata brucki* was present.

In the low prey density treatment, the percentage mortality of larvae of *C. septempunctata brucki* due to cannibalism or intraguild predation increased slightly to 93% (Fig. 2-2a), which is simi-

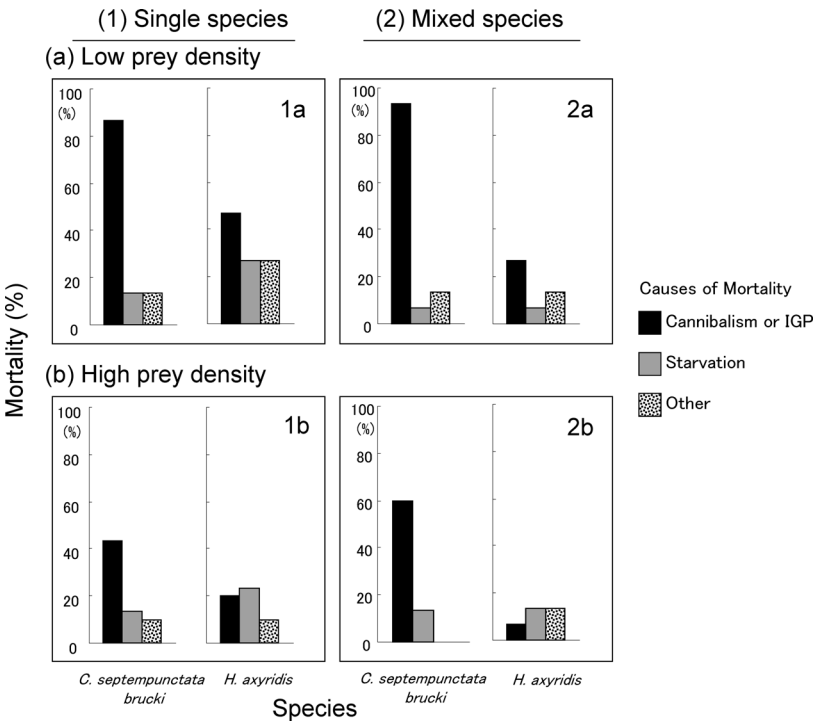

Fig. 2. Mortality rate of the larvae of two species of aphidophagous ladybirds, *C. septempunctata brucki* and *H. axyridis*, attributable to cannibalism or intraguild predation (IGP), starvation or other when reared in single or mixed species treatments at either a low or high prey population density.

lar to that in the single species experiment ($\chi^2=0.5$, d.f.$=1$, $p>0.05$) (Fig. 2-1a). In contrast, the percentage mortality of larvae of *H. axyridis* due to cannibalism or intraguild predation decreased by 20% (Fig. 2-2a), but the difference from that in the single species experiment was not significant ($\chi^2=1.7$, d.f.$=1$, $p>0.05$, Fig. 2-1a). Also, in the high prey density treatment, the percentage mortality due to cannibalism or intraguild predation in *C. septempunctata brucki* increased (Fig. 2-2b), whereas in *H. axyridis* it decreased; however, the differences between single and mixed species experiments were not significant (*C. septempunctata brucki*: $\chi^2=1.1$, d.f.$=1$, $p>0.05$; *H. axyridis*: $\chi^2=1.4$, d.f.$=1$, $p>0.05$); that is, the presence of other species differently affects the incidence of cannibalism or intraguild predation in these two species. In addition, 28 individuals died due to cannibalism or intraguild predation in mixed species experiments. Of these, 18 cases were observed, and *H. axyridis* was the intraguild predator and *C. septempunctata brucki* was the prey in all cases.

DISCUSSION

Our results indicate that cannibalism and intraguild predation were important mortality factors in intra- and interspecific relationships between two species of ladybird when aphids were scarce. *H. axyridis* was the intraguild predator and *C. septempunctata brucki* was its prey throughout larval development, particularly so during the latter developmental stages.

Body size, mobility, feeding specificity and prey abundance significantly affect the vulnerability of organisms to intraguild predation (Agarwala and Dixon, 1992; Lucas et al., 1998). The present study also indicates that prey abundance determines the incidence of intraguild predation and/or cannibalism. *Coccinella septempunctata brucki* and *H. axyridis* are similar in size (Yasuda and Kimura, 2001); however, in terms of feeding specificity *H. axyridis* is polyphagous and *C. septempunctata brucki* is more aphid-specific (Hodek and Honek, 1988; Lucas et al., 1997; Yasuda and Ohnuma, 1999; Sato et al., 2008). *Harmonia axyridis* is more aggressive and more successful in its attacks on conspecific or heterospecific individuals than *C.*

septempunctata brucki (Yasuda et al., 2001). In addition, in the present study, in all cases of intraguild predation observed, *H. axyridis* consumed *C. septempunctata brucki*. These results indicate that, in this system, *H. axyridis* is the intraguild predator and *C. septempunctata brucki* is its prey. The relationship between these two species is likely to be a consequence of differences in feeding specificity and predatory behavior.

Evans (1991) indicated that the magnitude of the effect of intra- and interspecific competition between species is similar, whereas Obrycki et al. (1998) shows that it depends on species. These interactions might differ due to the species involved. One of the objectives of our experiments was to determine the effect of competitive interactions between larvae of *C. septempunctata brucki* and *H. axyridis* on larval developmental time and adult size; however, it is likely that before interspecific competition occurred, *H. axyridis* larvae ate the *C. septempunctata brucki* larvae and, as a consequence, interspecific competition for food did not occur; therefore, in the interaction between these two species, intraguild predation might be more important than interspecific competition.

A field study of the population dynamics of *C. septempunctata brucki* and *H. axyridis* in Japan indicated that mortality during the fourth instar is a key stage in both species (Kindlmann et al., 2000). In the present experiments, the mortality of both species increased during the latter developmental stages; however, the experiments reported here were performed in enclosures, which prevented the predators from dispersing. Therefore, the results may not indicate the precise nature of the mechanism by which *H. axyridis* dominates this ladybird assemblage. In fact, a previous study showed that larvae of *C. septempunctata brucki* are more likely to emigrate from trees when aphids become scarce than *H. axyridis* (Sato et al., 2003), which suggests that dispersal by late stage larvae of *C. septempunctata brucki* could be an important factor determining their survival.

Cannibalism is common in predatory arthropods (e.g., Elgar and Crespi, 1992) and is frequently recorded in ladybirds (Mills, 1982; Osawa, 1989; Hodek and Honek, 1996); for example, in the wolf spider, *Schizocosa ocreata* (Hentz), cannibalism acts as a strong density-dependent mortality factor regulating the population density of this spider (Wagner and Wise, 1996) and similarly is also thought to contribute to the population regulation of dragonfly larvae (Van Buskirk, 1989; Hopper et al., 1996). In the present study, cannibalism was recorded in both species and was dependent on both prey abundance and developmental stage. As fourth instar larvae of *C. septempunctata brucki* and *H. axyridis* can often survive and develop to the adult stage by eating only conspecific larvae (Yasuda and Ohnuma, 1999), cannibalism is clearly advantageous when aphids become scarce. Previous analyses indicated that the key factor in the population dynamics of *C. septempunctata brucki* and *H. axyridis* is larval survival, particularly in the fourth instar (Osawa, 1993; Kindlmann et al., 2000). Thus, intraguild predation acting on *C. septempunctata brucki* and cannibalism in *H. axyridis* might be important factors determining the population dynamics of these two species.

Intraguild predation often occurs in aphidophagous guilds (Rosenheim et al., 1993, 1995; Cisneros and Rosenheim, 1997; Dinter, 1998; Lucas et al., 1998; Obrycki et al., 1998). In ladybird guilds, *H. axyridis* is thought to be a top predator (Dixon, 2000); therefore, in order to understand how *H. axyridis* affects the survival of other species in aphidophagous guilds it is important to have a better understanding of the ecology of all ladybirds in a guild.

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