



Interspecific interactions in a tri-trophic arthropod system: effects of a spider on the survival of larvae of three predatory ladybirds in relation to aphids

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Abstract

The effects of the crab spider, *Misumenops tricuspidatus* (Fabricius), on the larval survival of three ladybird species, *Hamonia axyridis* Pallas, *Coccinella septempunctata* L., and *Propylea japonica* L., in relation to aphids were investigated in the laboratory. Predation by the spider on the three ladybird species differed. All the larvae of *C. septempunctata*, none of *H. axyridis*, and an intermediate number of *P. japonica* were attacked and eaten by the spider. All the larvae of *H. axyridis* suffered mortality due to cannibalism or starvation in the treatments with and without a spider. In case of *C. septempunctata*, however, mortality in the early instars was significantly greater in the treatment with a spider than without a spider and no larvae developed into pupae due to predation. In the treatment without a spider, the majority of the larvae in the former treatment suffered mortality due to cannibalism or starvation, and only 13.3% of larvae developed into the adult stage. In the case of *P. japonica*, mortality was mainly attributed to predation in the treatment with a spider and only 26.7% became adult. In comparison, 86.7% of larvae survived to the adult stage in the treatment without a spider. In addition, in both *H. axyridis* and *C. septempunctata*, the development of young larvae was significantly slower in the presence of a spider, but this was not the case with the older larvae of *H. axyridis*, which indicates that the effect of the spider on larval development changed with the developmental stage of the larvae in this species. However, the spider had no significant effect on the developmental time of *P. japonica* larvae. Although both the spider and the ladybirds significantly affected the number of aphids, they did not have an additive effect on aphid abundance. The interactions between the spider and the ladybirds, such as intraguild predation or competition, caused them to reduce aphid population density less than the ladybirds did on their own. The effect of the spider on the larval performance of three predatory ladybirds was found to be unequal in terms of their vulnerability to predation and rate of larval development and it depended on the species and developmental stage of the ladybird.

Introduction

Food webs in a biological community can be very complex (e.g. Polis, 1991), and intraguild predation (IGP), in which potentially competing species often eat one another, greatly complicates our ability to evaluate the determinants of community structure (Polis et al., 1989; Polis & Holt, 1992). Therefore, to understand the determinant of the population density of each species in a community in terms of trophic

level interactions, it is necessary to describe the food web relationships between each species in a community. In addition, our understanding of community dynamics is also complicated by the fact that interspecific interactions between individuals change with their developmental stage.

Several species of aphidophagous insects may be attracted to the same patch of aphids (Sakuratani, 1977; Aalbersberg et al., 1988; Winder et al., 1994; Wyss, 1995), and a number of species of spiders may

also be present (Nyffeler et al., 1989; Wyss et al., 1995; Leather & Owuor, 1996). Recently, there has been an increasing awareness that IGP may play an important role in structuring aphidophagous communities (Rosenheim et al., 1993; Cisneros & Rosenheim, 1997; Ferguson & Stiling, 1996; Hirnori & Katsuhiko, 1997; Dinter, 1998; Lucas et al., 1998; Obrycki et al., 1998; Phoofolo & Obrycki, 1998). However, there are few studies of the interspecific interactions in tri-trophic systems, e.g. in systems that include a top predator like a spider.

In aphidophagous communities, ladybirds are important because of their voracity and diversity. IGP and cannibalism in ladybirds in the field are associated with a decrease in aphid abundance and an asymmetry in the vulnerability of the ladybirds (Hironori & Katsuhiko, 1997; Sato, 1997). Although spiders are generalist predators, they show a marked preference for a particular size and species of prey (Provencher & Coderre, 1987; Nyffeler et al., 1989; Spiller & Schoener, 1990). Thus, the outcome of the interactions between spiders and ladybird species is likely to depend on the stage of development and species involved.

On the host plant, *Hibiscus syriacus* L., at Tsuruoka, the cotton aphid, *Aphis gossypii* Glover, increases in abundance from the middle of May and an aphidophagous arthropod guild builds up. In particular, the three ladybirds *Harmonia axyridis* Pallas, *Coccinella septempunctata* L., *Propylea japonica* L., and a crab spider, *Misumenops tricuspidatus* (Fabricius) are common species as predators in the guild. In addition, *H. axyridis*-dominated ladybird assemblages are often observed on hibiscus trees in fields (Hironori & Katsuhiko, 1997; Sato, 1997), and this might be due to different effects of predation by a top predator like the crab spider on the survival of the ladybird species. In this assemblage IGP between *H. axyridis* and *C. septempunctata* larvae was reported (Hironori & Katsuhiko, 1997), but there is a lack of information on the interactions between ladybirds and spiders. To understand how the aphidophagous community is organized, food webs including interspecific interactions between predators involved have to be investigated. In this paper, four aspects of the interactions between three ladybird species and a crab spider are addressed experimentally, paying particular attention to the developmental stage of the ladybirds: (1) does the spider attack and eat the larvae of the ladybirds?, (2) do the ladybirds attack and eat the crab spider?, (3) does the spider affect the developmental

times of the ladybirds?, and (4) do these predators act on aphid abundance in an additive manner?

Materials and methods

The cotton aphid, *A. gossypii*, adults of the three ladybirds *H. axyridis*, *C. septempunctata*, *P. japonica*, and adult females of the crab spider, *M. tricuspidatus*, were collected from the host trees of the cotton aphid in the field at the Yamagata University. Adult ladybirds were fed on cotton aphids in plastic containers (15 cm in diameter and 9 cm high) and eggs laid by the females were collected every day. Each egg batch was put individually into a 9 cm Petri dish and the larvae were reared to the second instar on cotton aphids.

Branches of *H. syriacus* were cut from trees in the field at the end of March and rooted in rectangular pots in a greenhouse. Each branch was reduced to a height of 30 cm approximately ten weeks after planting, when they had fully expanded leaves, and branches were then planted individually in standard plant pots (10 cm in diameter and 10 cm high). Each branch was infested with approximately 200 adult cotton aphids and subjected to one of the following treatments, each replicated five times: (1) no predator; (2) a crab spider; (3) three second instar larvae of *H. axyridis*; (4) three second instar larvae of *H. axyridis* plus a crab spider; (5) three second instar larvae of *C. septempunctata*; (6) three second instar larvae of *C. septempunctata* plus a crab spider; (7) three second instar larvae of *P. japonica*; and (8) three second instar larvae of *P. japonica* plus a crab spider. A clear plastic cylinder (10 cm in diameter and 30 cm long) with one end covered with a nylon screen was placed over each branch. The numbers of individuals of aphids, larvae of the three ladybirds, and the spider tested in this experiment were within the range of numbers observed in the field (Sato, 1997). Spiders were starved for 24 h prior to an experiment in order to induce the same level of hunger, but the ladybird larvae were not starved. Total number of leaves per branch was similar within treatments and replications (14.1 ± 2.1 ($n=17$)). The experiment was designed to study the effect of predation by each of the three ladybirds *H. axyridis*, *C. septempunctata* and *P. japonica*, on the abundance of the aphids in the presence and absence of the crab spider.

Observations were made three times per day at 08:00, 13:00, and 18:00 until all the ladybirds were dead or had developed into adults. The numbers of

ladybirds alive, and whether they had moulted, were recorded at each observation, but the number of aphids was counted only at 13:00 each day. The weights of the ladybird larvae and adult spiders were measured to the nearest 0.01 mg using a Sartorius Type 1872 microbalance at the beginning of the experiment. After that, the ladybirds were reweighed just after moulting to the fourth instar and the spider on day 5. Gain in weight was calculated as follows:

$$\text{Gain in weight} = W_4 - W_2,$$

where W_4 = weight of fourth instar and W_2 = mean weight of second instar larvae at the beginning of the experiment. Percentage gain in weight of the crab spider was determined using the formula:

$$\text{Percentage gain in weight} = 100 \times (W_5 - W_1) / W_1,$$

where W_5 = weight of the spider on day 5 and W_1 = weight of the spider at the beginning of the experiment. The presence of a carcass of a ladybird larva with a small hole indicated it had been killed by the crab spider, whereas the absence of a carcass, or presence of pieces of a part of a carcass, indicated cannibalism. A shrunken carcass without a small hole indicated starvation.

All experiments, including the rearing of ladybirds, were carried out at a constant temperature of 25 ± 1 °C and a photoperiod of L 15:D 9 in a laboratory from 14 June to 23 July, 1996. A two-factor repeated measures ANOVA (with or without a spider and with or without ladybirds) was used to test for non-additive effects. Data were $\log(x + 1)$ transformed prior to analysis. Other data were analysed using one-way ANOVA or t-test, except the survival rates, which were analysed using χ^2 -test.

Results

Size of predators. The weight after moulting to the fourth instar of the three ladybirds in the treatment without a spider was 10.3 ± 0.8 mg ($n = 13$) in *C. septempunctata*, 11.5 ± 0.9 mg ($n = 14$) in *H. axyridis*, and 5.1 ± 0.5 mg ($n = 14$) in *P. japonica*, and that of the spider at the beginning of the experiment in the treatment without ladybirds was 25.8 ± 1.8 mg ($n = 20$).

Survival. The three ladybirds differed in their vulnerability to spider predation (Figure 1). No larvae of *H. axyridis* were eaten by the spider but all suffered

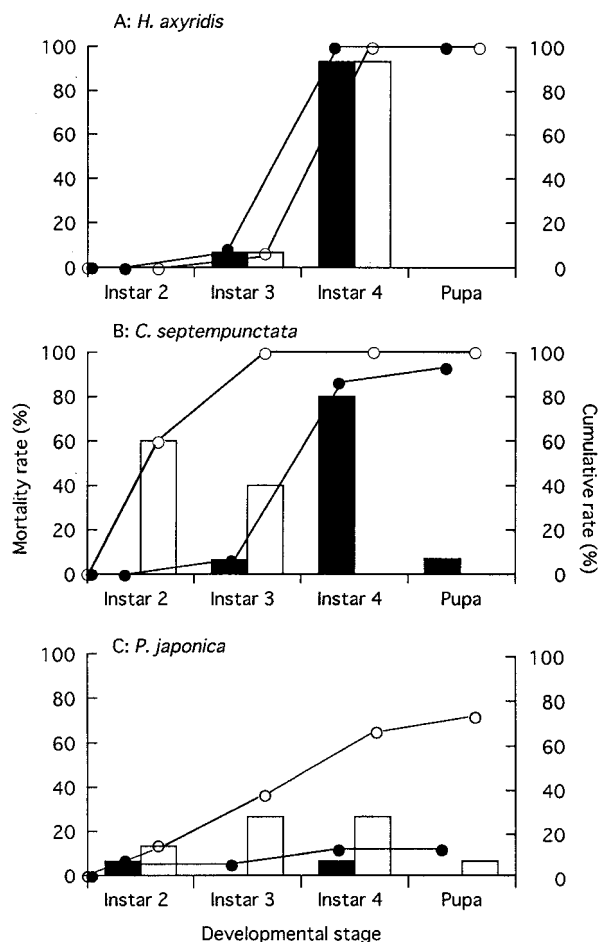


Figure 1. Mortality at each developmental stage of the three ladybird species in the presence and absence of a spider. Bars indicate ladybird mortality in the treatment with a spider (■) and without a spider (□). Circles show cumulative mortality in the treatment with a spider (●) and without a spider (○).

mortality due to cannibalism or starvation (Table 1). Most larvae of this species died during the fourth instar, and none pupated. In *C. septempunctata*, however, mortality in the early instars was significantly greater in the treatment with a spider than without a spider ($\chi^2 = 26.25$, $P < 0.01$). In the later treatment, the larva mortality was mainly due to cannibalism or starvation, and only 13.3% of larvae developed to the adult stage. In the case of *P. japonica*, an intermediate effect between the other two ladybird species was observed. In the treatment with a spider, the larval mortality was mainly attributed to predation by the spider and only 26.7% became adults. In comparison, 86.7% of larvae survived to the adult stage in the treatment without a spider.

Table 1. Causes of mortality of the three ladybirds in the presence and absence of spiders

	<i>H. axyridis</i>		<i>C. septempunctata</i>		<i>P. japonica</i>	
	No spider	Spider	No spider	Spider	No spider	Spider
Survivors	0	0	1	0	13	4
No. of individuals died	15	15	14	15	2	11
Cannibalism	8	9	8	0	0	0
Starvation	7	6	6	0	2	0
Predation by spider	–	0	–	15	–	11

Development. The mean developmental time of the three ladybird species is shown in Table 2. There was no significant difference in the developmental times of *P. japonica* in the presence or absence of a spider (to the third instar $t_{25} = 1.34$, $P > 0.05$; fourth instar $t_{21} = 0.76$, $P > 0.05$; pupa $t_{16} = 0.43$, $P > 0.05$; adult $t_{15} = 0.42$, $P > 0.05$). In the cases of *H. axyridis* and *C. septempunctata*, however, the duration of the second instar was significantly longer in the presence of a spider than in its absence (*H. axyridis*: $t_{28} = 2.63$, $P = 0.014$; *C. septempunctata*: $t_{19} = 3.31$, $P = 0.003$). However, there was no significant difference in the rate of development to the fourth instar in *H. axyridis* ($t_{26} = 0.511$, $P > 0.05$), indicating that the effect of the spider's presence on development changes with the stage of larval development in this species. There was no difference in the time taken to develop from the second to the third instar in these two species in the absence of a spider ($t_{28} = 1.14$, $P > 0.05$), however, in the presence of a spider *C. septempunctata* larvae took longer to develop than those of *H. axyridis* ($t_{19} = 2.68$, $P = 0.015$), suggesting that the effect of a spider on development was stronger in *C. septempunctata* than in *H. axyridis*.

When larvae of *H. axyridis* or *P. japonica* foraged for aphids in the presence of a spider, their gain in weight was not significantly different from when a spider was absent (*H. axyridis*: alone 9.5 ± 0.6 mg ($n = 14$), with a spider 11.1 ± 0.8 mg ($n = 14$), $t_{26} = 1.52$, $P > 0.05$; *P. japonica*: alone 5.0 ± 0.7 mg ($n = 14$), with a spider 5.3 ± 0.9 mg ($n = 9$), $t_{20} = 0.26$, $P > 0.05$). There were no significant differences in the percentage gain in weight of the spider in the four treatments (spider alone: 99.1 ± 3.1 mg ($n = 5$), with *H. axyridis*: 94.6 ± 4.9 mg ($n = 5$), with *C. septempunctata*: 107.4 ± 4.6 mg ($n = 5$), and with *P. japonica*: 104.4 ± 2.3 mg ($n = 5$), $F_{3, 16} = 2.13$, $P > 0.05$).

Aphid consumption. The mean number of aphids initially present per plant was similar in the eight treatments, ranging from 195.2 ± 2.0 to 215.6 ± 5.0 . Larvae of ladybirds and spiders rapidly consumed the aphids and their number decreased linearly during the course of the experiment (Figure 2). When kept without natural enemies, the number of aphids increased (Figure 2D). Although both the spiders and ladybirds significantly affected the number of aphids, except the effect of spider in the treatment with a spider and *C. septempunctata* (Table 3), the interactions between ladybirds and the spider were also significant. There was a significant spider by ladybird by time interaction in *C. septempunctata* and *P. japonica*, indicating that there was a non-additive effect of the natural enemies. This indicated that the spider interfered with the ladybirds, causing them to eat fewer aphids than when the ladybirds were on their own. In the case of *H. axyridis*, the interaction was not significant indicating that the spider had less effect on *H. axyridis*, than the other two species of ladybird.

Discussion

This study revealed that the spider had a different effect on each of the three ladybird species: the larvae of *C. septempunctata* were highly vulnerable to predation by the spider, larvae of *H. axyridis* were least vulnerable, and *P. japonica* larvae were intermediate between the two extremes.

Four mechanisms may account for this difference in IGP by the spider: (1) prey preference of the spider, (2) vulnerability of the ladybirds, (3) encounter rate with the ladybirds, and (4) extraguild prey density. Spiders differ in their ability to reduce the abundance of different species of phytophagous insects (Spiller & Schoener, 1990), e.g., the spider, *Pardosa amen-tata* (Cl.), prefers fruit flies to aphids (Toft, 1995)

Table 2. Mean developmental time in hours (\pm S.E.) of the three ladybird species in the presence and absence of spiders (Sample sizes in parentheses). Numbers in a column followed by the same letter do not differ significantly, $P > 0.05$

Treatment	Instar 2 \rightarrow Instar 3	Instar 2 \rightarrow Instar 4	Instar 2 \rightarrow Pupa	Instar 2 \rightarrow Adult
<i>H. axyridis</i> (Ha)				
Ha	32.8 \pm 3.6a (15)	77.4 \pm 4.2a (14)	–	–
Ha+spider	42.5 \pm 1.6b (15)	79.9 \pm 2.8a (14)	–	–
<i>C. septempunctata</i> (Cs)				
Cs	37.4 \pm 2.3a (15)	80.8 \pm 3.9 (14)	214.0 \pm 1.99 (2)	332 (1)
Cs+spider	52.6 \pm 4.6b (6)	–	–	–
<i>P. japonica</i> (Pj)				
Pj	21.5 \pm 1.1a (14)	73.3 \pm 4.8a (14)	145.2 \pm 4.0a (13)	232.0 \pm 5.1a (13)
Pj+spider	19.8 \pm 0.5a (13)	67.7 \pm 5.5a (9)	148.0 \pm 0.9a (5)	228.0 \pm 4.0a (4)

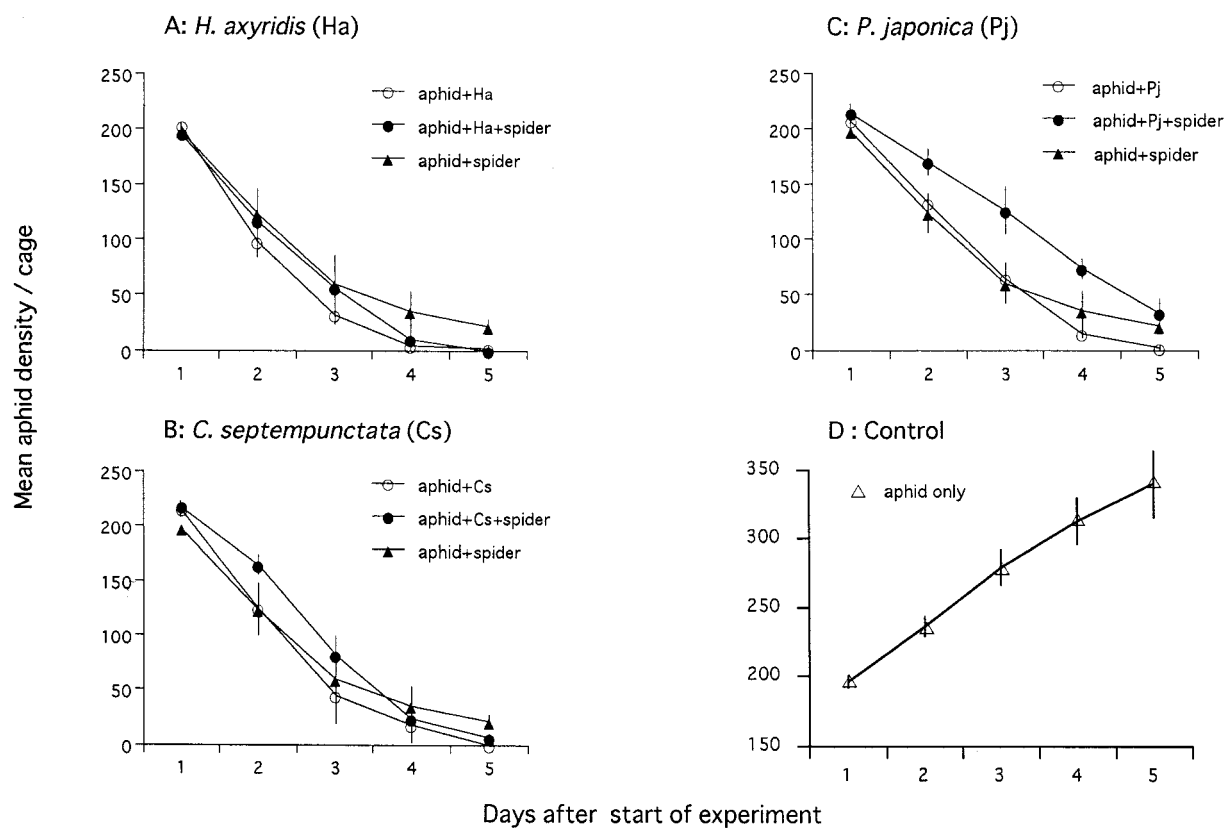


Figure 2. Mean (\pm SE) aphid density in the cages of each of the four treatments: aphids only (Δ), aphids and ladybirds (\circ), aphids and a spider (\blacktriangle), and aphids, ladybirds, and a spider (\bullet).

Table 3. Repeated-measures ANOVA on aphid densities for ladybird (+/–) and spider (+/–) treatments

Species	Source	df	ss	F	P
<i>C. septempunctata</i> (Cs)	Between subjects				
	Cs	1	10.611	84.618	<0.001
	Spiders (S)	1	0.343	2.742	0.101
	Cs×S	1	7.811	62.293	<0.001
	Within subjects				
	Time (T)	4	20.652	41.173	<0.001
	Cs×T	4	9.067	18.076	<0.001
	S×T	4	0.422	0.842	0.502
	Cs×S×T	4	3.562	7.103	<0.001
<i>H. axyridis</i> (Ha)	Between subjects				
	Ha	1	17.821	145.795	<0.001
	Spiders (S)	1	3.146	25.740	<0.001
	Ha×S	1	2.584	21.140	<0.001
	Within subjects				
	Time (T)	4	25.503	52.160	<0.001
	Ha×T	4	12.293	25.142	<0.001
	S×T	4	1.765	3.611	0.009
	Ha×S×T	4	1.178	2.411	0.055
<i>P. japonica</i> (Pj)	Between subjects				
	Pj	1	12.314	67.260	<0.001
	Spiders (S)	1	0.309	6.772	0.011
	Pj×S	1	7.978	174.310	<0.001
	Within subjects				
	Time (T)	4	12.314	67.260	<0.001
	Pj×T	4	4.260	23.273	<0.001
	S×T	4	0.167	0.914	0.459
	Pj×S×T	4	4.901	26.774	<0.001

and the spiders, *Tetragnatha laboriosa* Hentz and *Clubiona pikei* Gertsch, prefer certain aphids to others (Provencher & Coderre, 1987). As we did not study prey preference, we do not know whether the spider preferred a particular species of ladybird in this study. However, as all of the larvae of *C. septempunctata* and over 60% of those of *P. japonica* were eaten by the spider, it seems that these ladybirds are an acceptable prey. In the case of *H. axyridis*, it is likely that the spider is deterred from eating this species as no larvae were killed. In terms of vulnerability the larvae of *C. septempunctata* are more vulnerable to predation by conspecific or heterospecific larvae than are those of *H. axyridis* (Hironori & Katsuhiko, 1997), and *H. axyridis* larvae seem to be better defended than those of *C. septempunctata* (Yasuda, unpubl.). In other ladybird species or mosquito larvae, there are reports of

differences in their vulnerability to attacks by predatory ladybirds or predatory mosquito larvae (Agarwala & Dixon, 1992; Yasuda & Mitsui, 1992; Grill & Juliano, 1996). The longer sensory hairs of the larvae of *H. axyridis* may protect this species from an attack by the spider. Such a mechanism was also suggested for mosquito larvae (Bradshaw & Holzappel, 1983; Yasuda & Mitsui, 1992). Although we have no evidence of the relative vulnerability of *P. japonica* to attacks by other ladybirds, the fact that more than half of this species were attacked and eaten by the spider in this study indicates that this species is also a vulnerable species. The quantity of prey consumed by ladybirds is related to their size (e.g. Kawauchi, 1990). In terms of size *P. japonica* was the smallest species and, therefore, likely to consume the least food. That several larvae of *P. japonica* developed into adults even in

the treatment with a spider may indicate a lower encounter rate with the spider, due to the relatively low foraging activity of this species of ladybird. This is supported by the fact that a lot of aphids remained, even in the treatment with a spider, after the larvae had pupated. Extraguild prey density is known to affect the frequency of IGP (Johansson, 1993a; Dinter, 1998; Obrycki et al., 1998; Lucas et al., 1998). Although extraguild prey density was not different at the beginning of the experiments, the number of prey remaining at the end differed. This might also have contributed to the increased number of survivors of *P. japonica*. In the case of the larger ladybirds, a high food requirement led to a depletion of extraguild prey and an active foraging, which could have resulted in higher number of encounters with the spider. In summary, the variation in incidences of mortality in the three ladybirds is accounted for by the lower vulnerability of larvae in case of *H. axyridis* and a lower encounter rate associated with the low food requirement of the smaller species, *P. japonica*. The high mortality in *C. septempunctata* is possibly a consequence of their vulnerability and high foraging activity.

Symmetric IGP is the mutual predation of two predators on one another (Polis et al., 1989). In several species of arthropod predators, the younger individuals are sometimes preyed on by older individuals, and their vulnerability is dependent on their relative size and age (Moran & Hurd, 1994; Cisneros & Rosenheim, 1997; Lucas et al., 1998). In the present study, no spider was eaten by the ladybird. However, the larvae of *H. axyridis* are polyphagous (Hodek & Honek, 1988; Lucas et al., 1998; Yasuda & Ohnuma, 1999) and eat larvae of hoverflies, Lepidoptera, and even spiders (Sato, 1997). Therefore, it is suspected that depending on their age, availability of alternative prey, and the developmental stage of the spider, the older larvae of *H. axyridis* may feed on crab spiders.

The effects of the spider on the larval development of ladybirds may change as the ladybird increases in size, and such effects may differ between the three species. The crab spider affected the development of second instar larvae of *H. axyridis* and *C. septempunctata*, but it did not affect that of the third instar of *H. axyridis*. In addition, in the treatment without a spider, there was no difference in the time needed to reach the third instar in the two species, but in the treatment with a spider the development of *C. septempunctata* larvae was slower than that of *H. axyridis* larvae (Table 2) (Table 2). These results indicated that the spider interacted more strongly with *C. septempunctata* than with

H. axyridis. In the case of the treatment with a spider, the number of aphids per larva, after the beginning of the experiments, is likely to have been higher for *C. septempunctata* than for *H. axyridis* (Figures 1A, 1B and 2A, 2B), because of the reduced number of *C. septempunctata* larvae due to spider predation. A high food intake results in faster development of the larvae of *C. septempunctata* (Kawauchi, 1973) and *H. axyridis* (Hokusima & Ohwaki, 1972). The slower development of larvae observed in *C. septempunctata*, even in the treatment with high food availability, indicates that the crab spider interacted more strongly with *C. septempunctata* than with *H. axyridis* larvae which completed their development to fourth instar in the presence of a spider without any negative effect. In the case of *P. japonica*, the presence of a spider did not affect their development. After the beginning of the experiment, the number of aphids consumed in the treatment with *P. japonica* + spider was lower than in that where *P. japonica* was on its own (Figure 2C). As high food availability contributes to faster larval development in *P. japonica* (Kawauchi, 1979), the development in the treatment with a spider, in which food availability was high, possibly resulted from interaction with the spider. Although the spider affected larval development differently in the three ladybird species, the mechanism is not understood. As intraguild prey species may change their foraging behaviour in the presence of intraguild predators (Johansson, 1993a, b; Schmitz et al., 1997), this may influence the development of intraguild prey. Foraging behaviour of ladybirds, especially *C. septempunctata* and *P. japonica*, in the presence and absence of a spider, needs to be investigated.

In aphidophagous insects, IGP between the predatory hemipteran, *Zelus renardii* Kolenati, and the lacewing, *Chrysoperla carnea* (Stephens), results in an increase in aphid abundance through trophic cascades (Rosenheim et al., 1993; Cisneros & Rosenheim, 1997) and Dinter (1998) also suggests that this indirect effect by IGP might lead to an increase in aphids through the quadrifunctional interactions. Lucas et al. (1998) showed that the larvae of the lacewing, *C. rufilabris*, preyed on both the larvae of the ladybird, *Coleomegilla maculata* Timberlake, and of the gall midge, *Aphidoletes aphidimyza* Rondani, even in the treatment where the number of aphids was twice that necessary to sustain the predators, indicating that it is unlikely that these predators have an additive negative effect on aphid abundance. Furthermore, in aphidophagous guilds that include ladybirds and para-

sitoids, the effect of multiple natural enemies on aphid populations was non-additive due to IGP (Ferguson & Stiling, 1996), as in the present study. As these studies indicate that IGP is an important interaction in aphidophagous guilds, an additive negative effect of these predators and parasitoids on aphid abundance is not expected. That is, for a better understanding of the biological control of aphids, it is necessary to determine the nature of the interspecific interactions between the various members of an aphidophagous guild.

H. axyridis-dominated ladybird assemblages were observed on hibiscus trees in fields in northern Japan (Hironori & Katsuhiko, 1997; Sato, 1997) and the fact that no larvae of *H. axyridis* were eaten by the crab spider and their larval development was not affected in this study leads to the prediction that this ladybird has selective advantages in dominating the guilds of aphidophagous predators. We have some understanding of the IGP between the spider and the three ladybirds reported here, however, more complicated interspecific interactions are likely to occur, in particular between *H. axyridis* and the crab spider, since IGP between individuals may change with their developmental stage (Polis et al., 1989) and food availability (Moran & Hurd, 1994, 1997; Moran et al., 1996). Therefore, the next step of study should concentrate on the relationship between the two predators with the objective of understanding the dynamics of food webs in the aphidophagous community.

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