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Relationships Between Attack and Escape Rates, Cannibalism, and Intraguild Predation in Larvae of Two Predatory Ladybirds

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We compared incidences of cannibalism and intraguild (IG) predation (IGP) and quantified attack and escape rates—mechanisms which possibly account for the difference in incidences of these interactions—in laboratory experiments with Harmonia axyridis *and* Coccinella septempunctata. *There was a tendency for* H. axyridis *to act as an IG predator and* C. septempunctata *as an IG prey. Cannibalism was also often observed in both species. The incidences of both IGP and cannibalism were different between the species. The average attack rates of* C. septempunctata *were less than 20%, but those of the more aggressive* H. axyridis *exceeded 50%. Larvae of both species attacked conspecifics and heterospecifics* H. axyridis *larvae successfully escaped when attacked by both conspecifics and by heterospecifics, while larvae of* C. septempunctata *escaped from attacks of conspecifics but not from those of heterospecifics. Thus the aggressive behavior of* H. axyridis, *in particular, of the third and fourth instars, negatively affects the larval survival of* C. septempunctata. *It may contribute to the dominance of* H. axyridis *in ladybird assemblages and its displacement of other ladybird species in several places in the world.*

KEY WORDS: cannibalism; *Coccinella septempunctata; Harmonia axyridis*; intraguild predation; predatory ladybird.

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INTRODUCTION

Intra- and interspecific competition are important interactions among organisms which share the same food. Recently, cannibalism and intraguild predation (IGP) have attracted much attention, as it was shown that these interactions are significant and widespread among many taxa of predatory arthropods. They sometimes act as mechanisms of population regulation or as determinants of community structure (Polis *et al.*, 1989; Polis and Holt, 1992; Wagner and Wise, 1996; Holt and Polis, 1997).

Of 180 species of ladybirds in Japan (e.g., Sasaji, 1998), *Coccinella septempunctata* and *Harmonia axyridis* are the most widely distributed and common predators of aphids (e.g., Sakuratani, 1977; Takahashi and Naito, 1984; Osawa, 1993; Kawauchi, 1990; Hironori and Katsuhiro, 1997). They are effective predators which—due to their large size and therefore large prey consumption—are able to reduce aphid abundance. These two species exist in several habitats such as herbaceous plants and trees (Takahashi, 1989; Hodek and Honek 1996; Hironori and Katsuhiro, 1997; Brown and Miller, 1998; Colunga-Garcia and Gage, 1998). In northern Japan, overwintered adults of *C. septempunctata* emerge and lay eggs early in the season, when aphids appear only on trees, and *C. septempunctata* larvae coexist with later-appering *H. axyridis* larvae on trees (Hironori and Katsuhiro, 1997). *H. axyridis* is a widely polyphagous species, while *C. septempunctata* is a more aphid-specific predator (Hodek and Honek, 1988, 1996; Lucas *et al.*, 1997; Yasuda and Ohnuma, 1999). Cannibalism and IGP by *H. axyridis* and *C. septempunctata* larvae on the eggs, larvae, prepupae, and pupae of both these species in the field have been described often (Takahashi, 1989; Hironori and Katsuhiro, 1997; Sato, 1997).

Interesting interactions between *H. axyridis* and *C. septempunctata* in the field have been described in the United States: invasion of *C. septempunctata*, which replaced the native species (Elliott *et al.*, 1996), was followed by that of *H. axyridis*. The latter changed the structure of the ladybird assemblage dramatically again and resulted in *H. axyridis* replacing *C. septempunctata* as the dominant species (Brown and Miller, 1998). In northern Japan, the survival rate of *H. axyridis* was higher than that of *C. septempunctata* in the field for 4 years, which resulted in *H. axyridis*-dominated ladybird assemblages (Kindlmann *et al.*, 2000). Furthermore, it is suggested that cannibalism and IGP might be common and more important interactions in ladybird assemblages than intra- and interspecific competition (Yasuda *et al.*, 2001). Aggressive behavior of *H. axyridis* might contribute to the displacement of other ladybird species and to its dominance in ladybird assemblages. However, there are no studies showing the difference in predatory behavior such as attack or escape between the two species.

In this study, we compared incidences of cannibalism and IGP between *H. axyridis* and *C. septempunctata* and quantified attack and escape rates as the mechanism which possibly cause the difference in the incidences of these interactions. The incidences were compared not only between species, but also between instars, since the difference in larval instar between the two individuals involved may influence the result of their interactions (Agarwala and Dixon, 1992, Fincke, 1994; Snyder and Hurd, 1995; Lucas *et al.*, 1997).

MATERIALS AND METHODS

Cotton aphids, *Aphis gossypii*, and adults of the ladybirds, *C. septempunctata* and *H. axyridis*, were collected from the host tree, *Hibiscus syridis*, of the cotton aphid in the field at Yamagata University. Adult ladybirds were fed 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 individually placed in a 9-cm-diameter petri dish and the larvae were reared on cotton aphids. The rearing of ladybirds and the experiments were carried out at a constant temperature (25 $\pm$ 1°C) and photoperiod (L16:D8) in a laboratory.

Before the experiments, larvae were starved for 12 h to induce the same level of hunger. Each experiment consisted of 20 replications, in which two larvae were put in a 3-cm-diameter plastic petri dish without food, and during 1 h we observed the sequence of behavior from ladybirds coming into contact with each other through predation. The number of occurrences of each type of behavior was recorded. The possible sequences of behavior are shown in Fig. 1. Predation, attack, and escape rates were calculated by the following equations.

$$\text{Predation rate} = \text{Number of individuals eaten}/20$$

$$\text{Attack rate} = \text{Number of individuals attacked}/\text{Number of individuals contacted}$$

$$\text{Escape rate} = \text{Number of individuals escaped}/\text{Number of individuals attacked}$$

Each experiment included one combination of species (two individuals of the same species, one individual of each species) and instars (two same-instar larvae, two individuals differing in age by one instar). As a result, we carried out experiments with 32 combinations and 640 replications. As a younger larva has rarely eaten an older larva (only the third-instar larva of *H. axyridis* eating the fourth-instar larva of *C. septempunctata*), mainly the

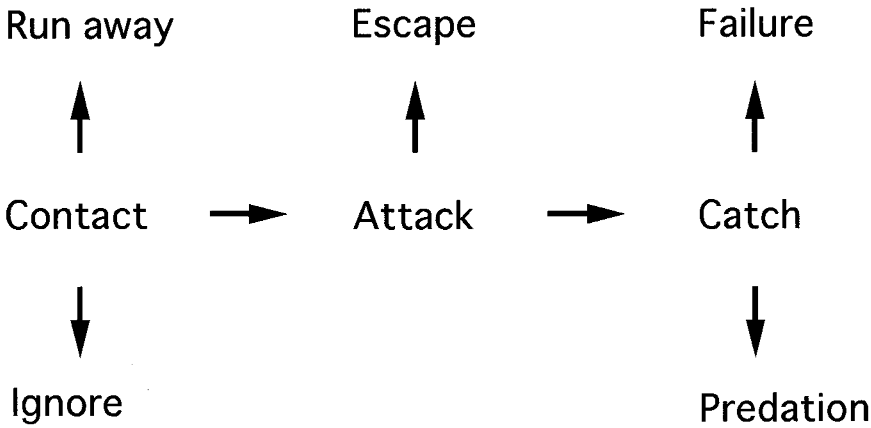

Fig. 1. Sequence of possible types of behavior, from ladybirds coming into contact with each other through predation.

relationships between same-instar larvae and between older and younger larvae are shown here.

Statistical analyses were conducted on mean predation, attack, and escape rates among treatments using ANOVA and mean differences separated using Fisher's protected least significant difference (PLSD). The data were arcsine-square root transformed before analysis.

RESULTS

Attack Rates

The mean attack rates of *C. septempunctata* were lower than those of *H. axyridis* ($F = 13.64$, $P < 0.0001$; Fig. 2). *C. septempunctata* larvae rarely attacked conspecifics. Its heterospecific attack rates were slightly higher than its conspecific attack rates, and the average rate was 20% (Fig. 2). On the other hand, *H. axyridis* was an aggressive species, with the average attack rates exceeding 50%. Especially the heterospecific attack rates were very high. Therefore, *H. axyridis* and *C. septempunctata* have different behavior in terms of attacking. In addition, the attack rates between old instars tended to be slightly higher than those between young instars (Fig. 3).

Escape Rates

Escape rates were usually high and exceeded 80%, irrespective of species and instar (Fig. 4). The only exception was the escape rate of

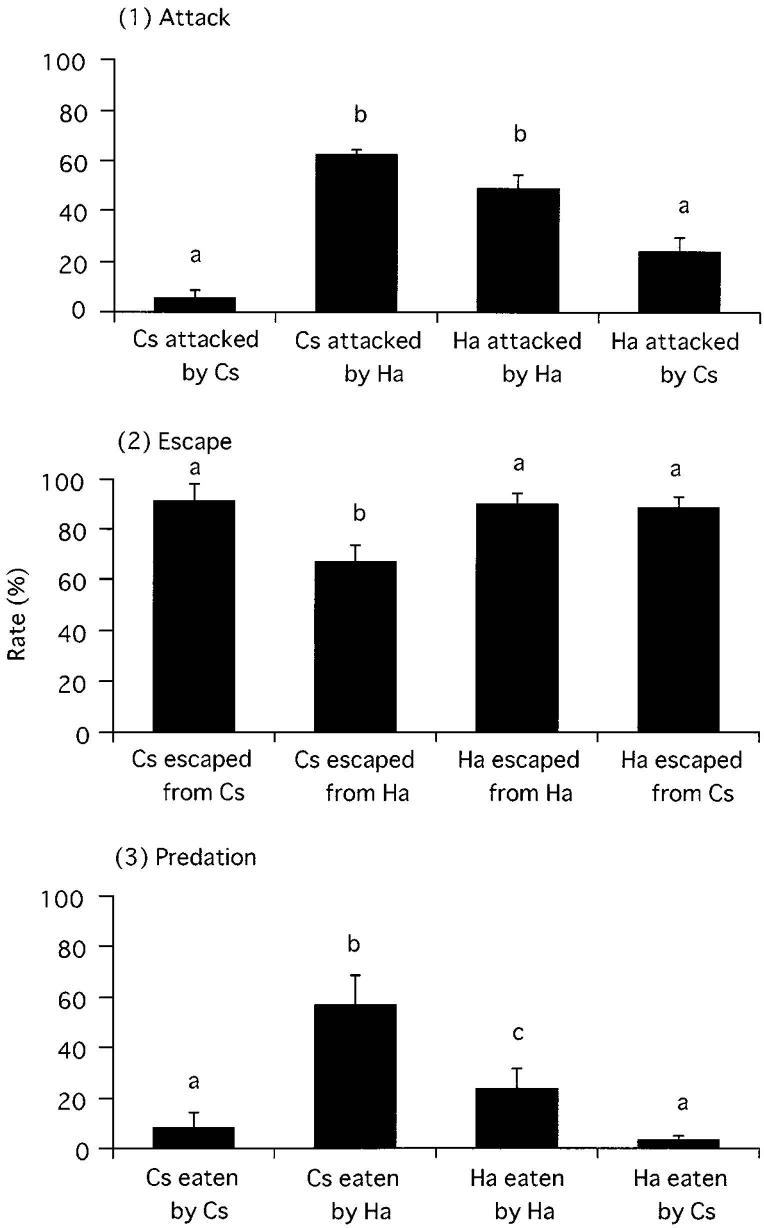

Fig. 2. Rates (mean ± SE) of individual ladybirds (1) attacked by, (2) escaped from, and (3) eaten by conspecifics or heterospesifics. Bars followed by different letters are significantly different (Fisher's PLSD test, $P < 0.05$). Cs, *C. septempunctata*, Ha, *H. axyridis*.

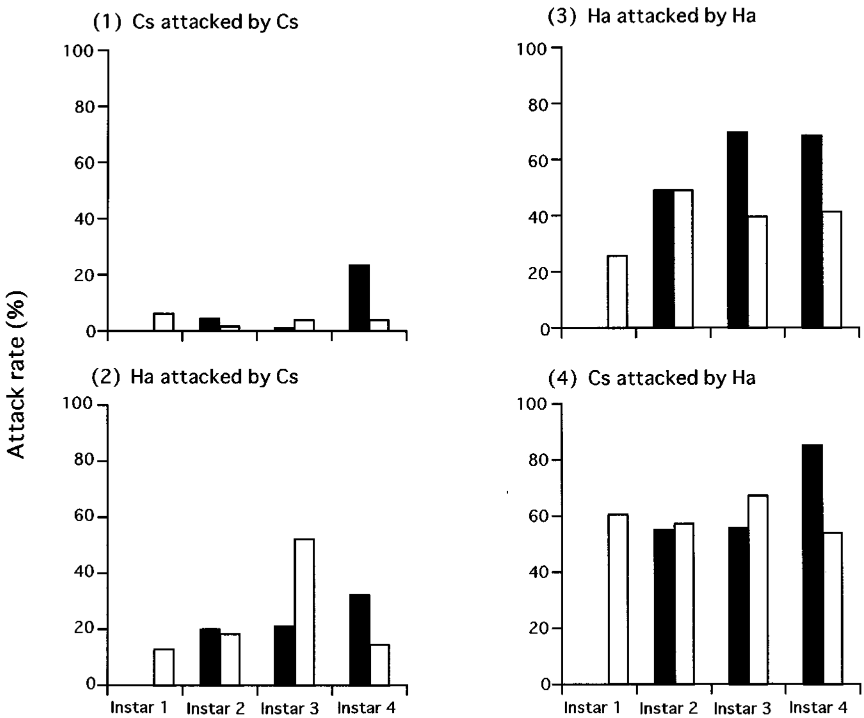

Fig. 3. Rate at which *C. septempunctata* (Cs) and *H. axyridis* (Ha) larvae were attacked by conspecific or heterospecific larvae. Solid bars represent cases when an old larva attacked a young one; open bars indicate attacks between same-instar larvae.

C. septempunctata after having been attacked by H. axyridis, which was significantly lower ($F = 4.08$, $P = 0.018$; Fig. 2), in particular, when *C. septempunctata* was attacked by the fourth-instar larvae of *H. axyridis*, when the rates were less than 60% (Fig. 4). Thus *C. septempunctata* was a more vulnerable species when being attacked by *H. axyridis*.

Predation Rates

The larvae of the two species were both cannibalistic, however, the incidence of cannibalism in *H. axyridis* was higher than that in *C. septempunctata* ($F = 11.75$, $P < 0.0001$; Fig. 2). In *C. septempunctata*, the fourth-instar ate the third-instar larvae; otherwise there was little cannibalism (Fig. 5). *H. axyridis* larvae, except for first instars, often cannibalized each other.

A striking difference in IGP between the two species was observed. The incidence of *H. axyridis* larvae preying on *C. septempunctata* larvae was high;

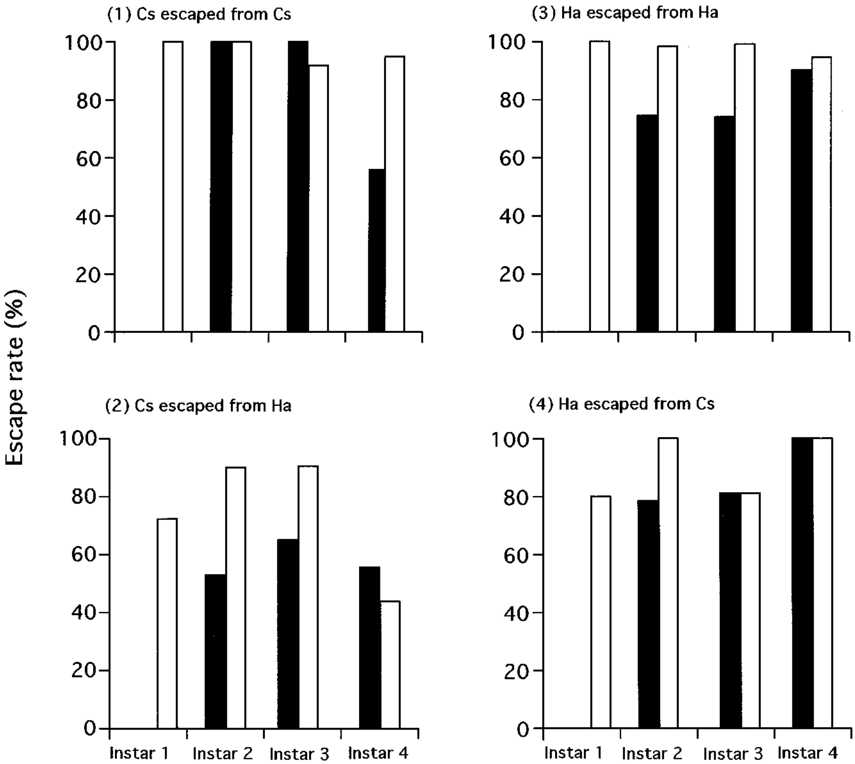

Fig. 4. Rate at which *C. septempunctata* (Cs) and *H. axyridis* (Ha) larvae escaped attacks by conspecific or heterospecific larvae. Solid bars represent cases when a young larva escaped from an old one; open bars indicate escapes between same-instar larvae.

in particular, 80% of *C. septempunctata* were eaten by fourth-instar larvae of *H. axyridis* (Fig. 5). However, it was rare for *C. septempunctata* to eat *H. axyridis*. The difference in incidence of IGP was significant between the two species ($F = 11.75$, $P < 0.0001$; Fig. 2). It is interesting that early-instar larvae of *H. axyridis* sometimes ate late-instar larvae of *C. septempunctata*; in particular, 15% of fourth-instar larvae of *C. septempunctata* were eaten by third-instar larvae of *H. axyridis*. However, earlier instars of *C. septempunctata* never ate later instars of *H. axyridis*.

DISCUSSION

Our experiments have precisely demonstrated for the first time the mechanisms in terms of the relationship between *H. axyridis* as an intraguild

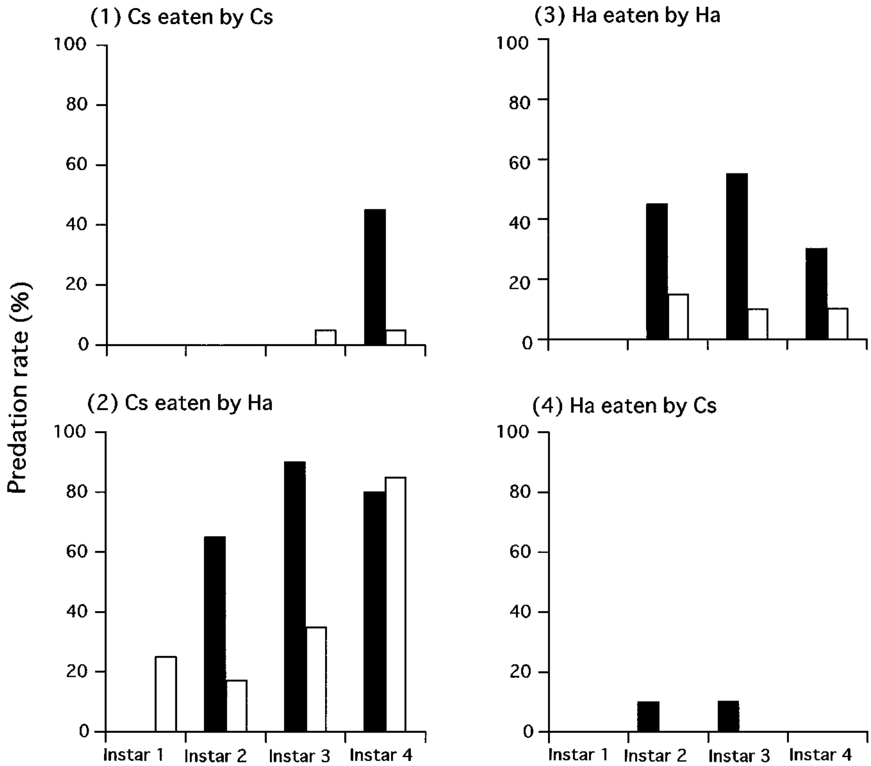

Fig. 5. Rate at which *C. septempunctata* (Cs) and *H. axyridis* (Ha) larvae were eaten by conspecific or heterospecific larvae. Solid bars represent cases when an old larva ate a young one; open bars indicate predation between same-instar larvae.

(IG) predator and *C. septempunctata* as an IG prey, although this relationship had already been observed in the field and quantified by enclosure experiments (Hironori and Katsuhiro, 1997; Yasuda *et al.*, 2001). Cannibalism has also been observed in both species before, but here the difference in the incidence between species was quantified for the first time.

The relationship between an IG prey and an IG predator was determined from the difference in attack and escape behavior between the two species. *H. axyridis* larvae often attacked earlier- or same-instar larvae irrespective of the species. *C. septempunctata* attacked other larvae less frequently than *H. axyridis* did. *C. septempunctata* attacked heterospecific larvae more than conspecific ones. Therefore, it seems that *H. axyridis* is a more aggressive species than *C. septempunctata*. The different response observed in *C. septempunctata* against conspecifics and heterospecifics is possibly attributable to the reaction of *C. septempunctata* larvae, in which the larvae were more frequently attacked by *H. axyridis* than by *C. septempunctata* larvae.

H. axyridis larvae successfully escaped from the attacks of not only conspecifics, but also heterospecifics. *C. septempunctata* larvae escaped from the attacks of conspecifics but not of heterospecifics. This is possibly attributable to the difference in morphology between the two species: *H. axyridis* larvae have sensory bristles on their body and a sucker-like attachment at the top of the abdomen, while *C. septempunctata* larvae do not. A difference in morphology in several insect species sometimes functions as a mechanism preventing capture by a predator (Bradshaw and Holzapfel, 1983; Yasuda and Mitsui, 1992; Volkl and Vohland, 1996). For instance, mosquito larvae of the genus *Orthopodomiya* are more resistant than *Aedes albopictus* against attacks by predatory *Toxorhynchites* mosquito larvae, and it is suggested that the longer, stout bristles of *Orthopodomiya* might decrease the strike–capture success ratio of the predators (Bradshaw and Holzapfel, 1983; Yasuda and Mitsui, 1992). In addition, Volkl and Vohland (1996) have shown that wax-covered larvae in ladybirds of the genus *Scymnus* are better protected against predation by larvae of other ladybird species than those without wax. The ability of *H. axyridis* larvae to fix their body on the bottom surface of the petri dish by the sucker seems to contribute to successful attack and escape behavior. Asymmetric IGP attributable to differences in behavior between the two species is also reported in IGP in pondskaters, *Gerris pingreensis* and *G. buenori*, in which capture by other gerrids was avoided due to a specific behavior (Spence and Carcamo, 1991). Therefore, the relationship between an IG prey and an IG predator in the two ladybird species is likely to be due to differences in aggressive behavior and in morphology.

In most cases of cannibalism or IGP, the difference in size determines the consequence of the interactions, in which smaller individuals are killed by large ones (Agarwala and Dixon, 1992; Fincke, 1994; Snyder and Hurd, 1995; Lucas *et al.*, 1997). In the case of *C. septempunctaia* and *H. axyridis*, there was no significant difference in size between same-instar larvae (Yasuda and Kimura, 2000). In this study, the incidence of cannibalism by old larvae on young ones tended to be higher than that between same-instar larvae. Successful IGP by fourth-instar *H. axyridis* occurred in more than 80% of cases, irrespective of the difference in size. However, large size was not advantageous in *C. septempunctata*; fourth-instar larvae of *C. septempunctata* were often attacked by third-instar larvae of *H. axyridis*, and 15% of *C. septempunctata* larvae were killed by the *H. axyridis* larvae. So, our results revealed that the aggressive behavior of *H. axyridis*, in particular, of the third and fourth instars, negatively affected the larval survival of *C. septempunctata*. In addition, it would contribute to its dominance in ladybird assemblages (Kindlmann *et al.*, unpublished) and its displacement of other ladybird species in several places in the world (Horn, 1996; Brown and Miller, 1998).

The feeding specificity of predators is also an important factor influencing the outcome of IG interactions. Lucas *et al.* (1998) suggested that specialist predators were more likely to become IG prey when involved in IG interactions. In the case of *C. septempunctata* and *H. axyridis, H. axyridis* larvae are more polyphagous than those of *C. septempunctata* (Hodek and Honek, 1988, 1996; Lucas *et al.*, 1997), and *C. septempunctata* is a more aphid-specific predator than *H. axyridis* (Yasuda and Ohnuma, 1999). Hence this study supports the hypothesis regarding the relationship between feeding specificity and outcome of IGP suggested by Lucas *et al.* (1998).

In this study, cannibalism and IGP were observed more often between old larvae than between young ones. We do not know whether old larvae are more aggressive than young larvae. However, as old larvae move faster in several species of ladybirds (Ng, 1988), the incidence of contact between the two individuals involved is higher between old larvae than between young ones, and this might result in the observed difference. In addition, starvation of the larvae in the 12 h preceding the experiment might have led to a higher level of hunger in old larvae because of their higher feeding rate and activity and, consequently, to a higher incidence of cannibalism and IGP between older individuals (Agarwala and Dixon, 1992; Lucas *et al.*, 1998).

IGP and cannibalism between the two ladybird species were known to be important in terms of intra- and interspecific interactions, but until now they had been studied only in limited taxa in arthropods (Polis *et al.*, 1989; Polis and Holt, 1992; Wagner and Wise, 1996; Holt and Polis, 1997). To find out whether cannibalism and IGP are widely distributed and common interactions in predatory communities, as suggested by Polis *et al.* (1989), these interactions should also be studied in other taxa, and not just in arthropods but also in invertebrates.

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