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SHORT COMMUNICATION

Effect of emigration on cannibalism and intraguild predation in aphidophagous ladybirds

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Abstract. 1. The incidence and timing of emigration, cannibalism, and intraguild predation of larvae of three aphidophagous ladybirds (Coleoptera: Coccinellidae), *Harmonia axyridis* Pallas, *Coccinella septempunctata brucki* Mulsant, and *Propylea japonica* Mulsant, relative to the presence of prey was determined in the laboratory in single- and mixed-species populations.

2. In single-species populations, 80% of the larvae of *C. s. brucki* emigrated prior to the extinction of the aphid population and no larvae were lost due to cannibalism; however >80% of the larvae of the other two species were still present when the aphid became extinct and the losses due to cannibalism for *H. axyridis* and *P. japonica* were 25% and 14% respectively. Finally, 28% of the *P. japonica* larvae completed their development, whereas no larvae of the other two species became adult.

3. In mixed-species populations, mortality of *P. japonica* attributable to cannibalism or intraguild predation increased greatly to 60%, whereas that of the other two species remained about the same. Consequently, survival of *H. axyridis* larvae improved and survival of *P. japonica* worsened; however the survival of *C. s. brucki* larvae was not affected by the other two species. Early emigration by *C. s. brucki* larvae may have enabled them to escape intraguild predation by *H. axyridis* in this system.

Key words. Aphid density, aphidophaga, cannibalism, emigration, intraguild predation.

Introduction

Intraguild predation is commonly observed in aphidophagous ladybirds (Coleoptera: Coccinellidae) and accounts for changes in ladybird guild structure. For instance, a restructuring of insect communities, in terms of species composition, appears to be occurring in aphidophagous ladybird guilds in the U.S.A. (Elliott & Kieckhefer, 1990; Elliott *et al.*, 1996). An introduced species, *Harmonia axyridis* Pallas, is invading aphidophagous ladybird guilds in North America (Day *et al.*, 1994; LaMana & Miller, 1996; Brown & Miller, 1998; Colunga-Garcia & Gage, 1998; McCorquodale, 1998), and intraguild predation by *H. axyridis* is thought to be an important force in structuring ladybird guilds (Yasuda & Shinya, 1997; Yasuda & Ohnuma, 1999; Kajita *et al.*, 2000).

In general, the incidence of cannibalism and intraguild predation by aphidophagous ladybird larvae is affected by the relative abundance of prey to larvae (Takahashi, 1987; Agarwala & Dixon, 1991, 1992; Yasuda & Shinya, 1997). Similarly, the incidence of larval emigration is also affected by prey abundance. In the field, larvae commonly leave a plant when prey becomes scarce (Yasuda & Shinya, 1997; Sato, 2001). This tendency of larvae to disperse when prey is scarce may further reduce the probability of encountering conspecific and heterospecific larvae (Schellhorn & Andow, 1999). In addition, the leaving rate depends on the species (Schellhorn & Andow, 1999). That is, when the incidence of cannibalism and intraguild predation is likely to increase, larvae tend to disperse from plants. Consequently, the incidence of cannibalism and intraguild predation is unlikely to be high in species that tend to emigrate early.

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In Japan, *H. axyridis* commonly co-occur with *Coccinella septempunctata brucki* Mulsant and *Propylea japonica* Mulsant (Takahashi & Naito, 1984; Yasuda & Shinya, 1997; Sato, 2001). Time of emigration of larvae of these three species of ladybird relative to extinction of aphids was monitored on shrubs in the field during spring 1995 and 1996 (Sato, 2001). Although several larvae of *C. s. brucki* and *H. axyridis* completed their development on the shrubs, a number of larvae emigrated in both species. Of the larvae that emigrated, $>90\%$ of *C. s. brucki* emigrated prior to the extinction of aphids, whereas $>70\%$ of *H. axyridis* larvae emigrated after the extinction of aphids. That is, if the tendency of larvae to disperse when prey is scarce reduces the probability of encountering conspecific and heterospecific larvae, as suggested by Schellhorn and Andow (1999), the incidence of cannibalism and intraguild predation is likely to differ in these two species.

In contrast to *H. axyridis* and *C. s. brucki*, no *P. japonica* larvae completed their development on the shrubs or emigrated. As several authors have suggested that intraguild predation is an important cause of mortality of larvae in the field (Osawa, 1993; Yasuda & Shinya, 1997), the disappearance of *P. japonica* is likely to be due to intraguild predation; however the time of emigration of this species is unknown, as none emigrated in this study.

As the effects of timing of emigration on the incidence of cannibalism and intraguild predation are poorly understood, it was decided to determine the relationship between larval emigration and survival in single- and multi-species ladybird guilds in the laboratory. In the work reported here, the effect of the presence of other species on the incidence of cannibalism or intraguild predation and emigration was determined by factorial experiments, using a combination of *H. axyridis*, *C. s. brucki*, and *P. japonica*.

Materials and methods

The effect of other species of ladybird on the survival of larvae that are free to emigrate was studied in an insectary during summer 1996. Young shrubs of *Hibiscus syriacus* L., 70 cm in height, were planted singly in pots (20 cm depth $\times$ 24 cm diameter) and each was fixed to a 60-cm steel stake. To water the shrubs and trap larvae that dropped from each shrub, a rectangular tray (10 cm deep $\times$ 40 cm wide $\times$ 70 cm long) filled with water was placed under each flowerpot. To trap emigrating larvae, the inside of the rim of the flowerpots was sprayed with a sticky material. In addition, these two types of trap prevented spiders and ants, which are potential predators of ladybird larvae (El-ziady & Kennedy, 1956; Itioka & Inoue, 1996; Voelkl & Vohland, 1996; Sloggett, 1999; Yasuda & Kimura, 2001), from foraging on the shrubs. Each shrub was infested with cotton aphids, *Aphis gossypii* Glover, on several occasions, by placing leaves infested with the aphid on the shrubs. This aphid commonly occurs on *H. syriacus* in the field. The experiment was started when the number of aphids on each shrub reached 700. There were two treatments: single- and mixed-species, using a combination of species. Nine larvae of one of three species, *H. axyridis*, *C. s. brucki*, and *P. japonica*, or three larvae each of the three species were placed on a shrub in the single- and mixed-species treatments respectively, i.e. the total number of larvae per shrub was nine, and the same in both treatments. The number of larvae on each shrub and their developmental stages were noted daily. The developmental stage of the larvae that emigrated was noted, then they were removed. When a larva is eaten, the anterior parts of its body, such as the head and prothorax, tend to be left. These larval remains were identified to species and developmental stage. The presence of aphids was checked for daily until they became extinct, which occurred approximately 1 week after the start of the experiment. Second-instar ladybird larvae, which were kept singly and starved for <12 h after moulting, were used to initiate all experiments. Single-species populations of *H. axyridis* and *P. japonica* were replicated four times; all other populations were replicated five times. The experiments were continued until all the larvae completed their development, were eaten, or emigrated. In general, the duration of the experiment after the extinction of aphids was about a week. Temperature and day length were not regulated during the experiments. Emigrating larvae were all caught by the sticky material, that is, none were observed in the water.

Statistical analyses

The average percentages of larvae that were present, had emigrated, and were lost to cannibalism or intraguild predation, were compared among the three species in single- and mixed-species populations using a Kruskal–Wallis test. All percentages were arcsine transformed.

In the experiments, only *H. axyridis* or *P. japonica* completed their development. For these two species, the total number of larvae that pupated was compared in single- and mixed-species populations using chi-square test.

Results and discussion

Single-species populations

The average percentages of larvae present, lost due to cannibalism and emigration, just prior to the extinction of the aphid and at the end of the experiment, were compared among species in the single-species populations (Fig. 1a). The percentage of larvae that emigrated was $80.0 \pm 17.4\%$ ($n = 5$) for *C. s. brucki*, which was seven times greater than that for the other two species (Kruskal–Wallis test: $\chi^2 = 7.8$, d.f. $= 2$, $P < 0.01$). Cannibalism rarely occurred prior to the extinction of the aphids (Kruskal–Wallis test: $\chi^2 = 2.3$, d.f. $= 2$, $P > 0.05$). Consequently, when the aphids became extinct, the average percentage of larvae that were present varied significantly among species (Kruskal–Wallis test: $\chi^2 = 7.8$, d.f. $= 2$, $P < 0.05$); it was $20.0 \pm 17.4\%$ ($n = 5$) for *C. s. brucki*, which was less than a quarter of that for the other two species.

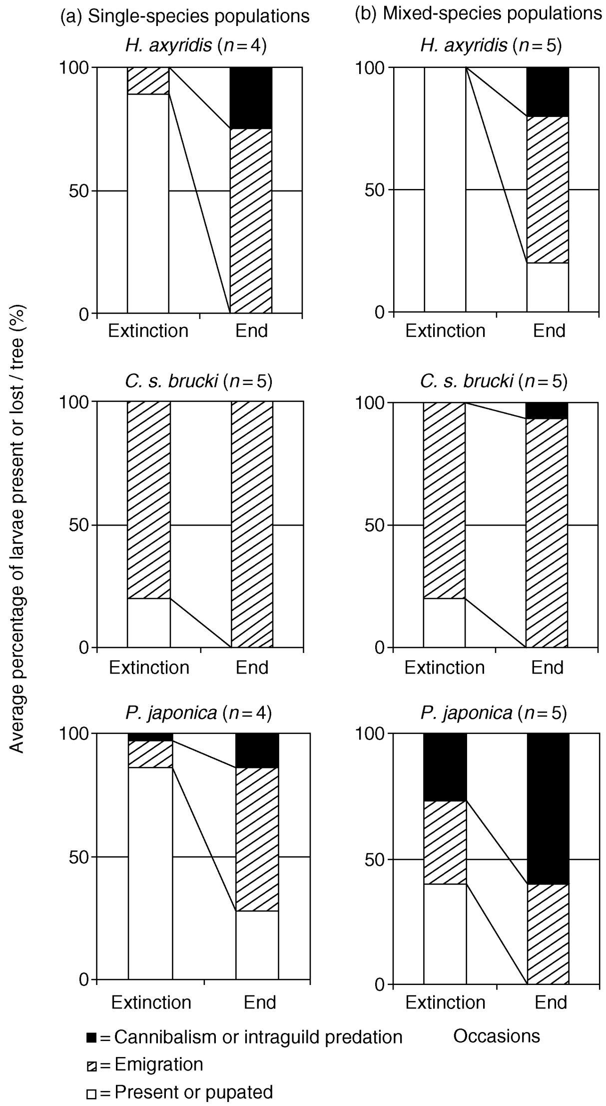

Fig. 1. Percentages of larvae that were present, lost due to emigration and cannibalism, or intraguild predation prior to the extinction of the aphid and at the end of the experiment in (a) single- and (b) mixed-species populations.

All larvae of *C. s. brucki* left plants prior to the end of the experiment, whereas the percentages of larvae that emigrated of the other two species did not exceed 75% (Kruskal–Wallis test: $\chi^2 = 8.0$, d.f. = 2, $P < 0.05$). The proportions of larvae lost to cannibalism prior to the end of the experiment varied significantly among species (Kruskal–Wallis test: $\chi^2 = 6.3$, d.f. = 2, $P < 0.05$), it tended to be higher in *H. axyridis* and *P. japonica* in this order, and no larvae of *C. s. brucki* was lost. The percentages of larvae that pupated varied significantly among species (Kruskal–Wallis test: $\chi^2 = 7.0$, d.f. = 2, $P < 0.05$), with only *P. japonica* completing its development.

Mixed-species populations

The average percentages of larvae that were present, lost to cannibalism or intraguild predation, or emigration prior to the extinction of the aphid, and at the end of the experiment, in mixed-species populations were also compared among species (Fig. 1b).

The percentage of larvae that emigrated prior to the aphid becoming extinct also varied significantly among species (Kruskal–Wallis test: $\chi^2 = 8.6$, d.f. = 2, $P < 0.05$); larvae of *C. s. brucki* were more likely to emigrate compared to the other two species. Although the percentage of larvae lost to cannibalism or intraguild predation did not vary significantly among species (Kruskal–Wallis test: $\chi^2 = 4.3$, d.f. = 2, $P > 0.05$), this cause of mortality was recorded only for larvae of *P. japonica*. The percentage of larvae that were present at the extinction of aphids varied significantly among species (Kruskal–Wallis test: $\chi^2 = 9.0$, d.f. = 2, $P < 0.01$); all larvae of *H. axyridis* were present, whereas the percentage of larvae that were present for the other two species decreased to less than 50%.

Although the percentages of larvae that emigrated (Kruskal–Wallis test: $\chi^2 = 5.2$, d.f. = 2, $P > 0.05$) and were lost to cannibalism or intraguild predation (Kruskal–Wallis test: $\chi^2 = 5.0$, d.f. = 2, $P > 0.05$) prior to the end of the experiment did not vary significantly among species, the apparent causes of larval loss varied. In *H. axyridis* and *C. s. brucki*, the loss was mainly due to emigration, whereas it was cannibalism or intraguild predation in *P. japonica*. Consequently, the percentage of larvae that pupated varied significantly (Kruskal–Wallis test: $\chi^2 = 7.0$, d.f. = 2, $P < 0.05$); only *H. axyridis* larvae completed their development.

Comparison of survival in single- and mixed-species populations

In these experiments, only *H. axyridis* or *P. japonica* completed their development. To determine the effect of the presence of the other species on survival, the numbers of larvae of these two species that pupated in single- and mixed-species populations were compared using chi-square test. In both species, there are significant differences in the total number pupating in single- and mixed-species populations (Chi-square test; *H. axyridis*: $\chi^2 = 7.7$, d.f. = 1, $P < 0.05$; *P. japonica*: $\chi^2 = 5.2$, d.f. = 1, $P < 0.05$); when other species were present the survival of *H. axyridis* improved and that of *P. japonica* worsened (cf. Fig. 1). Interestingly, the incidence of emigration by *C. s. brucki* up to the extinction of the aphid was similar in single- and mixed-species populations. That is, the presence of other species did not affect the timing of emigration in this species.

Emigration has been implicated as a factor reducing the incidence of cannibalism and intraguild predation. For instance, the incidence of cannibalism of pupae of *H. axyridis* is relatively low on plants remote from those on which the ladybirds developed (Osawa, 1993). In some species, 90% of the larvae leave plants prior to pupation

(Lucas *et al.*, 2000), and it is suggested that this emigration reduces the incidence of cannibalism and intraguild predation of pupae. For larvae, it is also likely that emigration reduces the incidence of larval cannibalism and intraguild predation when prey is scarce; however the effect of larval emigration on the incidence of predation has not previously been tested experimentally.

In general, the incidence of cannibalism or intraguild predation of ladybird larvae increases when the relative abundance of aphids to larvae is low (Takahashi, 1987; Agarwala & Dixon, 1991, 1992; Yasuda & Shinya, 1997). In the present experiments with single-species populations, however, the timing of emigration relative to extinction of aphids varied among species. Consequently, larval cannibalism was more likely to occur in species such as *H. axyridis* and *P. japonica*, which tended to stay on the shrubs when the aphids became extinct (Fig. 1). Of these species, however, only *P. japonica* completed its larval development. This is possibly because *P. japonica* is a relatively small species compared with *H. axyridis* and *C. s. brucki*, and requires less prey to complete its development. That is, there were sufficient aphids per shrub for some larvae of *P. japonica* to complete their development, but not for *H. axyridis* and *C. s. brucki*. In contrast to *H. axyridis* and *P. japonica*, cannibalism was not recorded for *C. s. brucki*, which tended to leave before the aphids became extinct. Therefore, it is likely that early emigration of *C. s. brucki*, relative to the extinction of its prey, reduces the incidence of larval cannibalism.

As an important factor determining species dominance in aphidophagous guilds, several authors have suggested that morphology and aggressiveness are important. For instance, Lucas *et al.* (1998) reported that lacewing larvae eat ladybird larvae and suggested that their greater aggressiveness or the shape of their mouthparts enables them to be an intraguild predator. In the ladybird species used in the present experiments, larvae of *H. axyridis* also have relatively large mandibles compared with those of the other two species (S. Sato, pers. obs.). In addition, Yasuda *et al.* (2001) reported that fourth-instar larvae of *H. axyridis* attack those of *C. s. brucki* more often per unit time than vice versa. That is, *H. axyridis* appears to be more aggressive than *C. s. brucki*.

Several studies indicate that *H. axyridis* larvae are well adapted to feed on other species and are well protected against predation. For instance, larvae of *H. axyridis* can complete their development or survive after feeding on eggs or larvae of other species of ladybird or aphidophagous predator, whereas those of *H. axyridis* appear to be unsuitable prey for other aphidophaga (Cottrell & Yeargan, 1998; Phoofolo & Obrycki, 1998) such as *C. s. brucki* (Yasuda & Ohnuma, 1999; Sato, 2001). It is suggested that some aphidophagous ladybirds are toxic (Agarwala & Dixon, 1992; Agarwala *et al.*, 1998; Hemptinne *et al.*, 2000) and this may be the way in which *H. axyridis* avoids intraguild predation. In contrast, *C. s. brucki* is not toxic to *H. axyridis* (Yasuda & Ohnuma, 1999; Sato, 2001). Accordingly, in the ladybird guild studied, *H. axyridis* larvae are potential intraguild predators of *C. s. brucki* larvae. In the present experiments, when there was no interaction between species, *H. axyridis* larvae did not complete their development; however when reared with other species under otherwise similar conditions, *H. axyridis* larvae completed their development. That is, *H. axyridis* acted as an intraguild predator of the other species; however as the incidence of cannibalism or intraguild predation of *C. s. brucki* larvae did not increase when other species were present, *C. s. brucki* was not an intraguild prey of *H. axyridis*. This is probably because all the *C. s. brucki* larvae emigrated prior to the extinction of the aphids, so their survival was not affected by the presence of other species of ladybird. That is, the early emigration of *C. s. brucki* may enable them to escape from intraguild predation by *H. axyridis* larvae. Interestingly, the incidence of early emigration of *C. s. brucki* was similar in single- and mixed-species populations.

In contrast, *P. japonica*, which tended not to emigrate prior to the aphids becoming extinct, became intraguild prey of *H. axyridis*, and enabled it to complete its development. In general, small species are more vulnerable to intraguild predation by large species than vice versa (Sengonca & Frings, 1985; Lucas *et al.*, 1998; Phoofolo & Obrycki, 1998; Hindayana *et al.*, 2001). Therefore, in the present study, *P. japonica*, which is smaller than *H. axyridis* and *C. s. brucki*, was possibly the most vulnerable species. In fact, survival of *P. japonica* larvae decreased when the other species were present, while that of *H. axyridis* larvae increased. As almost all of the *C. s. brucki* larvae had emigrated when the incidence of intraguild predation of *P. japonica* larvae increased, this predation is most likely attributable to *H. axyridis* larvae. However, *P. japonica* larvae would not be so vulnerable to intraguild predation by *H. axyridis* if they emigrated before the aphids became extinct. It is the relatively late emigration of *P. japonica* larvae that accounts for their high incidence of intraguild predation by *H. axyridis* larvae.

It is unknown why the timing of emigration relative to prey abundance varies among species. In general, the duration of aphid colonies is similar to that of the development of aphidophagous ladybirds (Dixon, 2000). Therefore, aphids are often likely to disappear before ladybird larvae complete their development when ladybirds do not lay eggs early in the development of a patch of prey. *Harmonia axyridis* and *C. s. brucki* have similar durations of development (Schanderl *et al.*, 1985; Kawauchi, 1990), however their timing of occurrence differs; *C. s. brucki* occur and lay proportionally more eggs earlier in the spring than *H. axyridis* (Takahashi & Naito, 1984; Yasuda & Shinya, 1997; Sato, 2001). Consequently, *H. axyridis* larvae are more likely to experience a scarcity of aphids than are *C. s. brucki* larvae. Therefore, to complete their development, *H. axyridis* larvae are more likely to depend on intraguild prey. This may account for why they are better adapted to eat prey other than aphids, which has been reported by several authors (Cottrell & Yeargan, 1998; Phoofolo & Obrycki, 1998; Yasuda & Ohnuma, 1999; Sato, 2001).

In conclusion, survival of ladybird larvae is likely to be affected by intraguild predation if they stay on plants where prey is scarce; however the survival of species that leave early is unlikely to be affected to the same extent by intraguild predation. Thus, it is important to take into account larval emigration when considering the potential interactions among species in aphidophagous guilds. The fact that the early emigration of larvae is a marked feature of some ladybirds indicates that it is adaptive. However, the fate of larvae after emigration is still unknown, and needs to be confirmed by more extensive and realistic experiments.

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