

CANNIBALISM AND INTERSPECIFIC PREDATION IN TWO PREDATORY LADYBIRDS IN RELATION TO PREY ABUNDANCE IN THE FIELD

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Life tables for two predatory ladybirds, *Coccinella septempunctata* and *Harmoina axyridis*, were constructed in two years in which prey abundance differed. The prey aphid, *Aphis gossypii*, was abundant on its primary host from late May to late June. Females of *H. axyridis* and *C. septempunctata* laid their eggs during the increase and peak in aphid abundance. The oviposition period of *C. septempunctata* started before and was shorter than that of *H. axyridis*. In both species, intraguild predation and/or cannibalism of the egg and fourth instar stages, but rarely of other developmental stages, were observed. Fourth instar larvae of *H. axyridis* had to complete their development when aphids were scarce more frequently than those of *C. septempunctata*. The highest frequency of intra- and interspecific predation was of fourth instar *H. axyridis* larvae. In terms of intraguild predation, the larvae of *H. axyridis* preyed on larvae of *C. septempunctata*, but the reverse was not observed. Percentage survival from egg to adult in *H. axyridis* was higher than in *C. septempunctata* in both years, and least in both species in the year of low aphid abundance. These results suggest that prey abundance influenced the frequency of cannibalism and intraguild predation, which were important in structuring this guild of ladybirds.

KEY-WORDS: Coccinellidae, life tables, intraguild predation, cannibalism, prey abundance, emigration.

Intraguild predation (IGP) and/or cannibalism have been recorded for predatory insects. Prey abundance seems to be an important factor determining the frequency of IGP and sometimes may be the most important force structuring predatory insect communities (Polis *et al.*, 1989; Dong & Polis, 1992).

In the field usually more than one species of aphidophagous insects are attracted to sites where aphids are abundant (Sakuratani, 1977; Aalbersberg *et al.*, 1988; Arakaki, 1992; Winder *et al.*, 1994). In these aphidophagous guilds, complex interactions including IGP and interspecific competition are likely to occur between the different species of predators (Evans, 1991; Agarwala & Dixon, 1992; Rosenheim *et al.*, 1993). So, it is of interest to consider the intensity and nature of the intra- and interspecific interactions between the predators in relation to prey abundance since these interactions may affect the structure of aphidophagous insect guilds.

In aphidophagous insect guilds, ladybirds are important because of their voracity and numbers of species. In ladybirds, egg cannibalism by larvae and adults in the field has been

recorded for several species (Mills, 1982; Takahashi, 1989; Osawa, 1989, 1992). There are very few field studies on mortality, including that due to IGP, during larval development. Knowledge of this mortality for several species of ladybirds, which coexist in the same habitat, is needed for a better understanding of the intra- and interspecific interactions between ladybirds and their role in shaping guild structure in ladybirds. This paper records the mortality experienced by two coexisting ladybirds, *Coccinella septempunctata* and *Harmonia axyridis*, based on life table analyses in two years of different prey abundance, and presented in terms of the effects of (1) IGP, (2) cannibalism, and (3) emigration. The effects of IGP and cannibalism on guild structure in ladybirds are discussed.

MATERIALS AND METHODS

The study site was located on the Yamagata University farm (38°43'N, 139°49'E). It consisted of about 100 trees of *Hibiscus syriacus*, which is the primary host of the aphid, *Aphis gossypii*. In 1993 five and in 1994 three trees of about 2m in height were selected for study. The locations of egg batches laid on the leaves of these trees were marked by painting or fixing a small plastic tag with wire to the stalks of the leaves and the numbers of eggs, larvae, pupae, and newly emerged adults were counted every day from the middle of May to the middle of July in 1993 and 1994. The mortality attributable to IGP, cannibalism or predation by arthropods other than ladybirds was recorded. Egg cannibalism by sibling first instar larvae was indicated by the presence of complete eggshell. Egg predation by older instar larvae or adults was indicated by the presence of only traces of eggshell. Therefore, except when egg predation was observed, the fate of the eggs was decided on basis of the size of the eggshell. It is difficult to identify the two species at the egg stage because their eggs are similar in size, colour, number in an egg mass and morphology. In 1993, the eggs were identified by means of the larvae that hatched from them. In 1994, a few eggs were removed from each egg mass and placed in Petri dishes at 25°C and a 14 photoperiod in the laboratory, and identified to species when the larvae hatched.

Aphid abundance was estimated by counting the numbers of aphids on ten leaves (1993) and five leaves (1994) of ten randomly selected twigs per tree every day.

Life tables were constructed following Kiritani and Nakasuji (1967). To investigate the emigration of larvae from the trees, a chloride vinyl pipe (12 cm in diameter, 7 cm in height) sprayed with a sticky material was placed around the base of each tree and the numbers of larvae caught were recorded every day. Both the inside and outside of each trap were sprayed but only the individuals stuck to the inside of the trap were considered emigrants. All emigrants were removed immediately and the sticky material was renewed every two or three days.

RESULTS

SEASONAL CHANGES IN THE NUMBERS OF APHIDS AND LADYBIRDS

In the two years, aphids were observed on the trees from the middle of May until the middle of June (fig. 1 and 2). The peak number of aphids in 1994 was 1.5 times larger than in 1993. Females of *H. axyridis* and *C. septempunctata* laid eggs during the increase or peak of aphid abundance. Oviposition by *C. septempunctata* started earlier and lasted for a shorter period than that of *H. axyridis*. There were more eggs and larvae of *H. axyridis* than

of *C. septempunctata*. Most fourth instar larvae of *H. axyridis* developed after the disappearance of aphids in 1993 or when aphids were scarce in 1994, suggesting that the larvae of *H. axyridis* can complete their development when aphids are scarce. In contrast the fourth instar larvae of *C. septempunctata*, they were present when aphids were still abundant. For both species, the number of second instar larvae recorded was smaller than that of the other instars. This was most likely a consequence of sampling error since it was more difficult to find second instar larvae because of their size and tendency to disperse.

LIFE TABLES OF LADYBIRDS

In *C. septempunctata*, egg mortality was 43.1% in 1993 and 47.5% in 1994 (table 1). Larval mortality was highest in the fourth instar. No newly emerged adults were observed in 1993, but in 1994, 17 individuals reached adulthood and the total mortality was 95.4%. In *H. axyridis*, egg mortality was 47.0% in 1993 and 46.3% in 1994 (table 2). The highest larval mortality was in the fourth instar in both years and total mortality to adult emergence was 98.9% in 1993 and 92.9% in 1994. In both species, the highest levels of mortality occurred in the fourth instar. Pupal mortality was lower in *H. axyridis* than in *C. septempunctata*. The total mortality in both species was lower in 1994 than in 1993. In 1994, aphids were more abundant (fig. 1 and 2) and the number of eggs laid by both ladybirds was smaller than that in 1993 (tables 1 and 2). Therefore, the lower total mortality in 1994 suggests that a higher prey density per ladybird larva results in higher survival rate in both species.

Mortality was caused by IGP, cannibalism, and predation by spiders. In *C. septempunctata*, predation by *H. axyridis* larvae was the major mortality factor, whereas cannibalism by conspecific larvae seemed to be the most important mortality factor in *H. axyridis*. *C. septempunctata* was never observed attacking *H. axyridis*, suggesting that the predatory relationship between the two species is asymmetrical.

Although both third and fourth instar larvae of both species emigrated from trees, more fourth than third instar larvae did so. This may be also related to the decrease in aphid abundance during fourth instar (fig. 1 and 2).

DISCUSSION

This study showed that cannibalism and IGP occurred during the egg and fourth instar larval stages, but were rare in other developmental stages. Although fourth instar larvae of *H. axyridis* often ate conspecific and/or heterospecific larvae, those of *C. septempunctata* rarely did so and prey abundance influenced the frequency of cannibalism and IGP.

In predatory ladybirds, cannibalism by larvae and adults is observed in several species and its frequency is affected by prey abundance (Takahashi, 1987; Osawa, 1992; Agarwala & Dixon, 1991, 1992). The oviposition strategy of ladybirds determines the degree of synchronization between the presence of larvae and availability of aphid prey, which is important for larval survival. In some ladybirds, females lay their eggs before the peak in aphid abundance (Hemptinne *et al.*, 1992), *H. axyridis*, however, did not always lay its eggs during the increase in aphid abundance and as a consequence their larvae often experienced poor food availability, especially during the fourth instar. As in predatory ladybird guilds the fate of the larvae may be decided by IGP or cannibalism, depending on aphid abundance, it is important to study the oviposition strategies of the component species of the guild (Dixon, 1996).

Though several studies have shown that egg cannibalism is common in ladybirds (Kawai, 1978; Mills, 1982, Takahashi, 1987; Osawa, 1989, 1992; Agarwala & Dixon, 1991), there

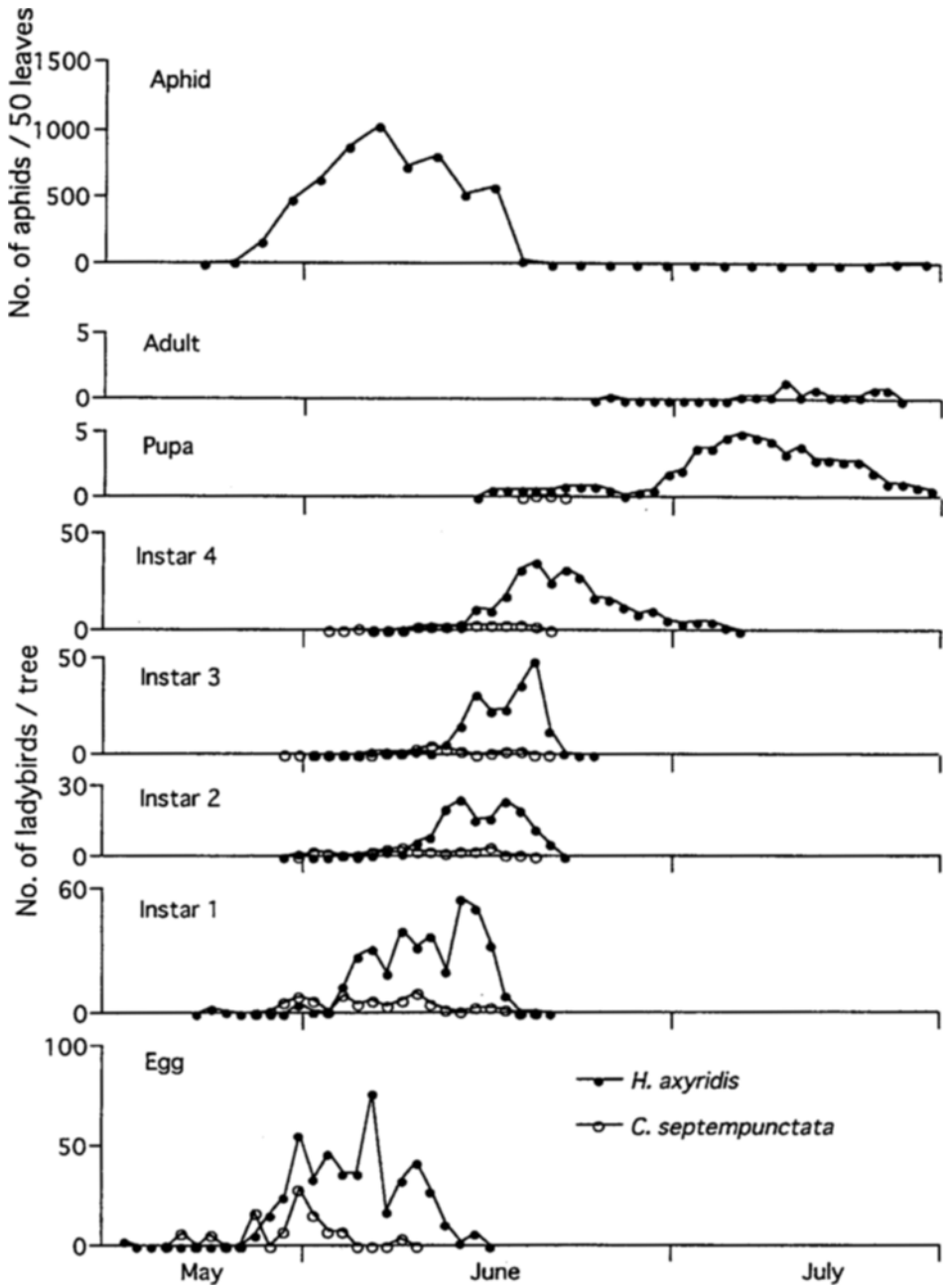


Fig. 1. Seasonal changes in the number of aphids and two species of ladybirds in 1993.

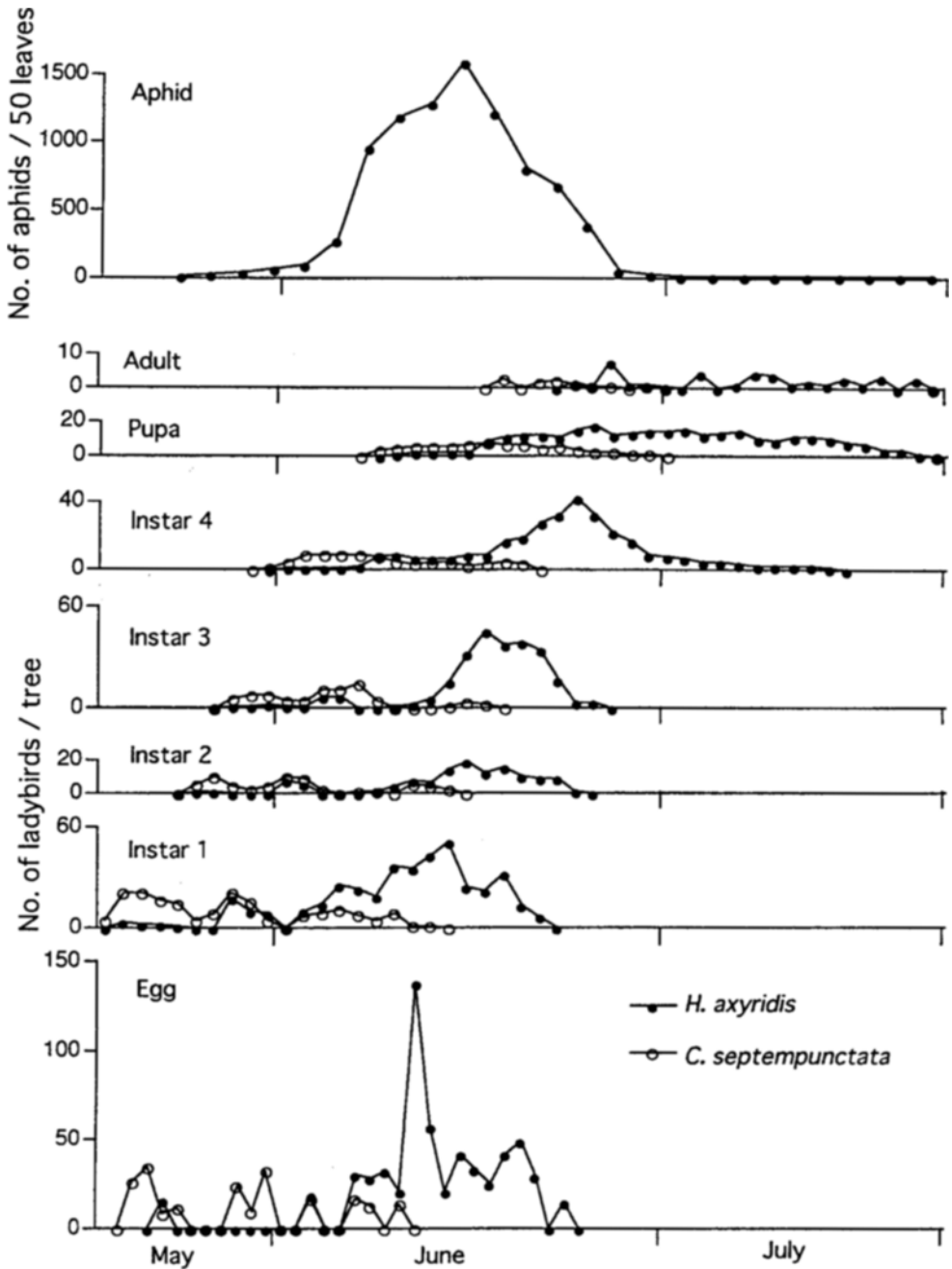


Fig. 2. Seasonal changes in the number of aphids and two species of ladybirds in 1994.

TABLE 1
Life tables of *C. septempunctata* for 1993 and 1994

| Stage (x) | 1993 | | | | 1994 | | | | |
|-----------|---|---|------------------------|--------------------------|----------|-----|---|---------------|--------------------|
| | Number observed at start of each stage (lx) | Factor responsible for dx (dxF) | No dying during x (dx) | dx as (%) of lx (100 qx) | x | lx | dx F | dx | 100 qx |
| eggs | 441 | Cannibalism by siblings Unhatched Unknown | 40 21 129 | 9.1 4.8 29.2 | eggs | 366 | Cannibalism by siblings Unhatched Unknown | 8 6 160 | 2.2 1.6 43.7 |
| | | Total | 190 | 43.1 | | | Total | 174 | 47.5 |
| Instar 1 | 251 | Unknown | 137 | 54.6 | Instar 1 | 193 | Unknown | 69 | 35.9 |
| Instar 2 | 114 | Unknown | 45 | 39.5 | Instar 2 | 123 | Unknown | 23 | 18.7 |
| Instar 3 | 69 | Unknown | 37 | 53.6 | | | | | |
| Instar 4 | 32 | Predation by Ha larva Unknown | 1 30 | 3.1 93.8 | Instar 3 | 100 | Predation by Spider Emigration Unknown | 1 1 24 | 1.0 1.0 26.0 |
| | | Total | 31 | 96.9 | | | Total | 26 | 28.0 |
| Pupa | 1 | Predation by Ha & Cs larva* | 1 | 100 | Instar 4 | 74 | Predation by Spider Emigration Unknown | 1 6 43 | 1.4 8.1 58.1 |
| | | Total | 1 | 100 | | | Total | 50 | 67.6 |
| Adult | 0 | Total mortality | | 100% | Pupa | 24 | Predation by Ga larva Unknown | 3 4 | 12.5 16.7 |
| | | Total mortality | | 100% | Adult | 17 | Total | 7 | 29.2 |
| | | Total mortality | | 100% | | | Total mortality | | 95.4% |

* Ha: *H. axyridis*, Cs: *C. septempunctata*.

TABLE 2
Life tables of H. axyridis for 1993 and 1994

| | | 1993 | | | | 1994 | | | |
|----------|------|------|--|--------|----------|------|---------------------------------------|-----|--------|
| x | lx | dx | F | 100 qx | x | lx | F | dx | 100 qx |
| eggs | 2348 | 277 | Cannibalism by siblings unknown* | 11.8 | eggs | 1481 | Cannibalism by siblings unknown | 226 | 15.3 |
| | | 45 | Predation by Cs larva | 1.9 | | | Unknown | 122 | 8.2 |
| | | 13 | Unhatched | 0.6 | | | Unknown | 30 | 2.0 |
| | | 177 | Unknown | 7.5 | | | Total | 308 | 20.8 |
| | | 592 | | 25.2 | | | Unknown | 685 | 46.3 |
| Instar 1 | 1244 | 1104 | Total | 47.0 | Instar 1 | 796 | Unknown | 247 | 31.0 |
| | | | Cannibalism by Ha larva | 0.1 | Instar 2 | 549 | Emigration | 1 | 0.2 |
| | | | Predation by Spider | 0.1 | | | Unknown | 80 | 14.6 |
| | | | Unknown | 39.5 | Instar 3 | 468 | Total | 81 | 14.8 |
| | | | Total | 39.7 | | | Emigration | 7 | 1.5 |
| Instar 2 | 751 | 493 | Unknown | 27.7 | | | Unknown | 83 | 17.7 |
| Instar 3 | 543 | 208 | Cannibalism | | Instar 4 | 378 | Total | 90 | 19.2 |
| | | | by Ha larva | 0.2 | | | Cannibalism by Ha larva | 12 | 3.2 |
| | | | Predation by Spider | 0.2 | | | by Ha adult | 2 | 0.5 |
| | | | Unknown | 44.2 | | | unknown | 6 | 1.6 |
| | | | Total | 44.6 | | | Emigration | 31 | 8.2 |
| Instar 4 | 301 | 242 | Cannibalism | | | | Unknown | 210 | 55.6 |
| | | | by Ha larva | 4.0 | | | Total | 262 | 69.3 |
| | | | Unknown | 83.0 | | | Cannibalism by Ha larva | 3 | 2.6 |
| | | | Total | 87.0 | | | unknown | 5 | 4.3 |
| Pupa | 39 | 263 | Cannibalism by Ha larva | 12.8 | Pupa | 116 | Unknown | 3 | 2.6 |
| | | | Unknown | 20.5 | | | Total | 11 | 9.5 |
| | | | Total | 33.3 | Adult | 105 | Total mortality | | 92.9% |
| Adult | 26 | 13 | Total mortality | 98.9% | | | Total mortality | | |

* Whether by conspecific or heterospecific unknown.

are few studies of interspecific egg predation except in the laboratory (Agarwala & Dixon, 1992). Agarwala & Dixon (1992) showed that the frequency of interspecific egg predation and the mortality of predators from eating eggs differs between ladybirds, as the eggs of some species appear to be more protected chemically against predation. *C. septempunctata* ate the eggs of *H. axyridis*, but the reverse was not observed in this study. This may imply that the eggs of *C. septempunctata* are protected against predation by *H. axyridis*. The first instar larvae of some ladybirds can develop to the second instar on a diet of eggs and in several species, eggs are better food than aphids (Kawai, 1978; Takahashi, 1987; Osawa, 1989, 1992; Agarwala & Dixon, 1991, 1992). Egg cannibalism in ladybirds is thought to have evolved because there are no penalties associated with eating conspecific eggs (Agarwala & Dixon, 1992). Most egg predation in the present study was due to cannibalism and the frequency of egg cannibalism in *H. axyridis* was higher than in *C. septempunctata*. Banks (1957) suggested that species with large egg clusters have a higher frequency of egg cannibalism, however, the numbers of eggs in the egg clusters of *C. septempunctata* and *H. axyridis* do not differ (Sato & Yasuda, unpubl.). Egg cannibalism in *C. septempunctata* is rare if the larvae are provided with an abundance of aphid prey (Takahashi, 1987), however, *H. axyridis* larvae prefer their eggs to aphids (Kawai, 1978). Therefore, the marked egg cannibalism in *H. axyridis* may depend on the species specific predation behaviour of *H. axyridis*.

In this study, cannibalism and asymmetrical IGP were observed. The incidence of cannibalism was very dependent on the age of the predator and stage of development of the prey as recorded in other ladybirds and predatory insects (Takahashi, 1987; Agarwala & Dixon, 1992; Yasuda & Hashimoto, 1995). In respect of IGP, vulnerable species are known from laboratory studies (Agarwala & Dixon, 1992). Though IGP in ladybirds has been recorded in the laboratory, it has not been observed in the field except for larvae eating pupae where fourth instar larvae of *H. axyridis* have been observed eating pupae of *C. septempunctata*, but not the reverse (Takahashi, 1989). The larvae of *H. axyridis* are polyphagous (Hodek & Honek, 1988). We observed that they preyed on larvae of hoverflies, lepidopterous larvae, and even spiders (Sato & Yasuda, unpubl.) and the larvae of *C. septempunctata* were more vulnerable to predation than those of *H. axyridis* (Kikuchi & Yasuda, unpubl.). Therefore, the asymmetrical IGP may be related to the differences in food specificity and vulnerability between the two species.

Emigration was dependent on prey abundance. Though the fate of emigrants was unknown, the likelihood of the emigrants surviving is low because there were few trees or plants with high numbers of aphids on the study site at the time of emigration. As low prey abundance promotes the movement of ladybird larvae, this induced activity may lead to an increase in the frequency of cannibalism and/or IGP.

The response of predators to prey abundance can be classified as a functional or a numerical response (Solomon, 1949). A number of studies have reported functional responses in predatory insects (Hokyo & Kawauchi, 1975; Matura & Morooka, 1983; Spitze, 1985; Hubbard *et al.*, 1988; Zheng *et al.*, 1993a, b; Yasuda, 1995). The numerical response except for the oviposition behaviour of the ladybird, *Adalia bipunctata*, in relation to prey abundance (Mills, 1982; Hemptinne *et al.*, 1992), has been poorly studied as it is difficult to determine the numbers of predators and their prey in the field (Matura, 1976). In addition, in biological communities, whether the primary control in trophic interactions is through the availability of resources or by predation is still being debated (Power, 1992). A better understanding of the numerical relationship between predator and prey would aid the debate. Survival from egg to adult in both ladybirds was higher when aphids were relatively

abundant. Although long term field studies are needed to clarify the relationship between predator and prey abundance, the present study indicates that the number of prey determines the number of predators in the field.

IGP and cannibalism have been observed in a number of animals and are seen as a force for structuring predatory insect communities (Polis *et al.*, 1989; Dong & Polis, 1992). The guild structure in ladybirds was investigated in a long term field study in north America by Elliott *et al.* (1996). Though the structure changed when the introduced *C. septempunctata* invaded the study area, the mechanism by which the change occurred is unknown (Elliott *et al.*, 1996). Osawa (1993) suggests that cannibalism is important for the stability and persistence of *H. axyridis* populations, and the larval mortality is a key factor in their population dynamics. However, the factors causing larval mortality are unknown. In the present study, survival rate was higher in *H. axyridis* than in *C. septempunctata* in the two years and asymmetrical IGP between *H. axyridis* and *C. septempunctata* larvae was observed. In addition to the small number of spiders that caused some larval mortality, several unknown factors also contributed to larval mortality, however, the most important factors structuring the ladybird guild in this study were cannibalism and IGP. This hierarchy in IGP is likely to be a general phenomenon and an important force for structuring the guild of ladybirds.

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RÉSUMÉ

Cannibalisme et prédation interspécifique au champ chez deux coccinelles prédatrices en relation avec l'abondance de la proie

Des tables de survie pour deux coccinelles prédatrices, *Coccinella septempunctata* et *Harmonia axyridis*, ont été établies au cours de deux années où l'abondance en proies était différente. La proie, *Aphis gossypii*, était abondante sur l'hôte primaire de la fin mai à la fin juin. Les femelles d'*H. axyridis* et de *C. septempunctata* ont pondu leurs œufs pendant la période de multiplication et le pic d'abondance des pucerons. Par rapport à *H. axyridis*, la période d'oviposition de *C. septempunctata* a débuté plus tôt et a été plus courte. Chez les deux espèces, on a observé la prédation intra-guille et/ou le cannibalisme du stade œuf et du 4^e stade larvaire, mais rarement celui des autres stades de développement. Les larves du 4^e stade d'*H. axyridis* ont dû, plus souvent que celles de *C. septempunctata*, achever leur développement alors que les pucerons devenaient rares. La fréquence de prédation inter- et intraspécifique la plus élevée a été observée chez les larves du 4^e stade d'*H. axyridis*. En termes de prédation intraguilde, les larves de *H. axyridis* peuvent se nourrir des larves de *C. septempunctata*, mais l'inverse n'a pas été observé. Le taux de survie de l'œuf à l'adulte a été plus élevé chez *H. axyridis* que chez *C. septempunctata* durant les deux années, et plus faible chez les deux espèces l'année où les pucerons étaient moins abondants. Ces résultats suggèrent que l'abondance des proies influe sur la fréquence du cannibalisme et de la prédation intraguilde, ce qui est important dans la structuration de cette guilde de coccinelles.

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