Effects of prey density and spatial distribution on prey consumption of the adult predatory ladybird beetle

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Abstract: The effects of prey density and spatial distribution on prey consumption of the adult predatory ladybird, *Harmonia axyridis*, were investigated by using a 2 × 2 factorial design in large scale cages. Prey density influenced prey consumption of the ladybirds, and the frequency with which predation occurred was quite different between the prey distributions. The ladybirds consumed a relatively constant and small number of aphids when the prey were uniformly distributed, whereas the number of prey consumed per day when predation occurred was large and much more variable when the prey were contagiously distributed. At high prey density, the number of prey consumed was highest during the first day of the experiment; thereafter, only 10–20 aphids were consumed during the following 3 days. However, these patterns of prey consumption were not observed at low prey density. The percentage of aphids that remained on the host plants when the experiments were terminated was higher at low prey density than at high prey density, suggesting that predator foraging efficiency at low prey density was lower than at high prey density. Ladybirds foraging for high prey density were more frequently observed on the plants with aphids than ladybirds foraging for low prey density. Prey distribution also influenced the frequency of residence of ladybirds on the plants. The different predation patterns observed in the two spatial distributions, in which prey consumption was much more variable for the contagious distribution, might be explained by the difference in prey encounter rate of the predator between the distributions. This study indicated that the ladybirds had limited ability to search out prey over large spatial scales.

1 Introduction

Prey density and spatial distribution are of crucial importance in determining the rate at which predators consume their prey (IVLEV, 1955; MURAKAMI and TSU-BAKI, 1984; CAPPUCCINO, 1987). Because the amount of prey consumed affects development, survival, and reproduction of predators (e.g. MATSURA and MOROOKA, 1983; ZHENG et al., 1993a,b; YASUDA, 1995), one must study predator responses to these factors to understand the ecology of predators, including their searching behaviour, foraging efficiency, and prey consumption.

Predatory ladybirds prey on a number of species of aphids on different host plants with variable prey density and spatial distribution among seasons and places (e.g. SAKURATANI, 1977; WINDER et al., 1994). Although most adult ladybirds aggregate in areas of high aphid density (MILLS, 1982; SAKURATANI et al., 1983; KAREIVA, 1984; OBATA and JOHKI, 1990; EVANS and YOUSSEF, 1992; IVES et al., 1993), the amount of prey consumed may vary with foraging efficiency, which is affected by prey density and its distribution.

Foraging efficiency of ladybirds is influenced by several factors such as plant structure (CARTER et al., 1984), plant architecture (GREVSTAD and KLEPETKA, 1992), and habitat quality (CARTER and DIXON, 1982). In addition to these factors, MURAKAMI and TSUBAKI (1984) have shown that the effect of prey distribution on the foraging efficiency of *Coccinella septempunctata* larvae is changed by prey density (MURAKAMI and TSUBAKI, 1984). In several ladybirds, area-concentrated prey searching behaviour after prey consumption is well known for adults (BANKS, 1957; DIXON, 1959; CARTER and DIXON, 1982; NAKAMUTA, 1982, 1985; MURAKAMI and TSUBAKI, 1984), and there are also studies on intensive searching behaviour of coccinellid larvae (MARKS, 1977; CARTER and DIXON, 1984). Prey recognition is reported by several workers for *C. septempunctata* adults, which can visually recognize prey individuals at short distances (NAKAMUTA, 1984, 1985), and for *Harmonia axyridis* adults, which use both olfactory and visual cues to detect a prey individual before actual contact occurs (OBATA, 1986).

Although a number of studies on foraging behaviour in ladybirds have already been carried out in the laboratory, most of these studies are for larvae and the experimental area is small in size. Scale is an important issue in the study of prey consumption by predators in relation to prey density or its distribution (KAREIVA, 1986; GASCON and TRAVIS, 1992; IVES et al., 1993) because differences in spatial scales may influence predator responses to variation in these factors. However, there are few large scale experimental studies on the effects of these factors on prey consumption of adult ladybirds. Such studies are important because the amount of prey consumed by adult females affects the number of eggs laid (KAWAUCHI, 1990) and because foraging adult females decide the oviposition site which will determine their fitness (DIXON, 1996). However, our understanding of behaviour of adult ladybirds is incomplete.

This study explores the effects of prey density and spatial distribution on foraging behaviour and prey consumption of the adult ladybird, *H. axyridis*, by using a factorial design on a large spatial scale.

2 Materials and methods

Experiments were carried out on *H. axyridis* adults. Pupae or fourth instars of this species were collected from *Hibiscus syriacus*, the primary host tree of the cotton aphid, *Aphis gossypii*, in the field. Larvae were fed three species of aphids, *A. gossypii*, *Myzus persicae*, and *Macrosiphoniella sanborni*, which held in plastic containers (15 cm in diameter and 9 cm in height) the bottom of which was lined with filter paper. Containers were held at a constant temperature ($22 \pm 0.5°C$) and a photoperiod of 16 h light (L) : 8 h dark (D) in the laboratory. Newly eclosed adults were obtained from these cultures and were used for experiments. Adults were chosen from the containers at random without distinction of the sexes.

Eggplants were used as the foraging substrate in the experiments. Each eggplant was grown individually in a columnar pot (15 cm in diameter and 20 cm in height) in the greenhouse to a height of 50 cm. These plants were trimmed of excess leaves such that four large leaves remained at the beginning of the experiment. Each pot with an eggplant was placed in a plastic container (25 cm in length, 35 cm in width, and 5 cm in height) the bottom of which was lined with wet paper to prevent the escape of aphids that dropped into the container from the plant. Experiments were conducted by placing nine potted eggplants with their plastic containers in a 3×3 arrangement with adjustment containers separated by 15 cm from each other. The set of nine plants was covered with a $1 m \times 1 m \times 1 m$ iron pipe frame screened cage.

Experiments were conducted in a 2×2 factorial design with five replications, with the two factors being prey density and spatial distribution. Prey densities were 36 and 180 aphids, *A. gossypii*, per cage and spatial distributions were contagious and uniform. In the contagious distribution, all aphids (36 or 180) were placed on the central plant, whereas in the uniform distribution each of the nine plants in the cage received the same number of aphids (four or 20). The aphids were allowed to settle on the plants for 1 day before the experiments were started. Offspring produced during this day were removed before the experiment was started. A Petri dish with nine adult ladybirds was hung from the centre of the cage and these ladybirds were released from the Petri dish into the cage. Initially, most ladybirds landed on the side of the cage.

The number of ladybirds on individual plants was recorded every hour from 0600 to 1800 h after the experiments were started, and the numbers of aphids on the plants and aphids in the plastic container (i.e. those that had dropped from the plant) were counted every day during four successive days. The number of prey consumed was estimated by subtracting the numbers of aphids remaining on the plants or appearing in the bottom container on a given experimental day from the number of aphids present on the previous experimental day. Frequency of 'cage-days' of predation during these experimental days was determined by estimating the number of aphids consumed as 'non-0'. These experiments were carried out from 11 July to 13 August 1993 in a iron-screen-covered hut.

Two-way analysis of variance (ANOVA) was used to test the effect of the two factors on the number of prey consumed. The number (n) of prey consumed was log (n + 1) transformed prior to statistical analysis. Mean differences were separated with Tukey's honestly significant difference (HSD) multiple comparison test. The frequency of observations in which lady-
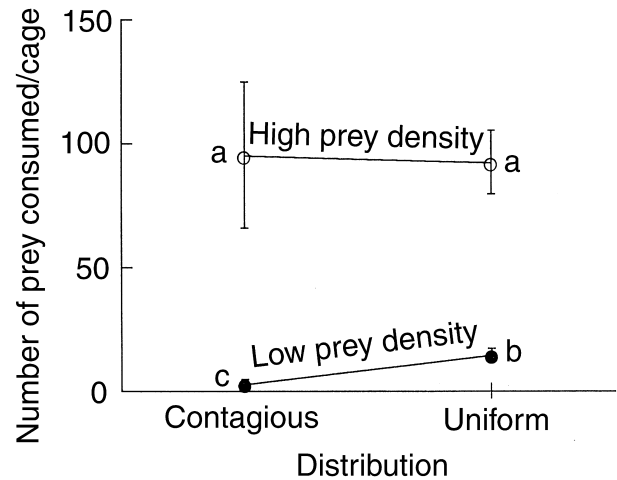

Fig. 1. *Mean number of prey consumed (SE) by ladybirds at each treatment during four experimental days. Symbols labelled with the different letter are significantly different based on Tukey's HSD multiple comparison test*

Table 1. ANOVA *results for the number of prey consumed by ladybirds (data log (n + 1) transformed)*

Source of variation	d.f.	MS	F	P
Density	1	6.07	21.13	P < 0.01
Distribution	1	2.02	7.04	P < 0.05
Density × distribution	1	0.51	1.77	NS

birds occurred on the plants with aphids was analysed using χ^2 test.

3 Results

3.1 Number of prey consumed

Ladybirds exposed to high prey density ate a larger number of aphids than those exposed to low prey density (fig. 1 and table 1). At low prey density, prey consumption given a uniform prey distribution was higher than that for contagious prey distribution (P < 0.01), but no similar prey consumption rates were observed at high prey density for the two prey spatial patterns (P > 0.05). At high prey density, the percentages of aphids that remained on the plants at the termination of the experiments were 28% for contagious prey distribution and 29.0% for uniform prey distribution. At low prey density the percentages were 43.1 and 45.8% for the contagious and uniform prey distribution. The percentage of aphids that remained at low prey density was higher than that at high prey density ($\chi^2 = 3.56$, d.f. = 1, P = 0.059), suggesting that ladybird foraging efficiency at low prey density was lower than that at high prey density.

At high prey density, the number of prey consumed was largest on the first day of the experiment; thereafter, only 10–20 aphids per cage were consumed during the
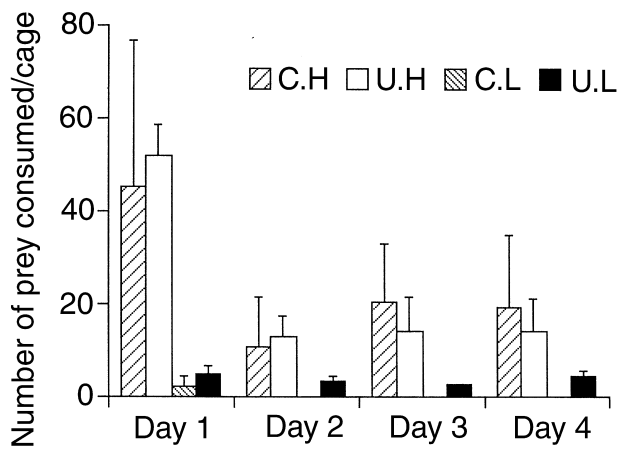
Fig. 2. *Mean number of prey consumed (SE) by ladybirds at each experimental day. C, contagious; U, uniform; H, high density; L, low density*

following 3 days (fig. 2). However, these patterns of prey consumption rates were not observed at low prey density. It is interesting to note the differences in the variance (SE) in prey consumption per day at high prey density (fig. 2); prey consumption in the contagious distribution was much more variable than in the uniform one.

3.2 Frequency of predation

Prey density and spatial distribution influenced the frequency with which predation occurred (table 2). Predation was observed almost every day in each replicate cage for the uniform distribution, but the number of days when predation occurred in the contagious distribution was significantly less than that in the uniform one (P < 0.01). In the contagious distribution, the number of days with predation was larger at high prey density than at low prey density (P < 0.01), but no such effect of prey density was observed in the uniform distribution (P > 0.05).

Predation in the contagious distribution with low prey density was observed on only 1 day in one replicate cage even though there were 20 possible 'cage-days' of predation during these experiments. This prevents testing whether differences in mean numbers of prey consumed on days with predation occurred between this treatment and others (table 2). Excluding this treatment, the number of prey consumed per day when predation occurred in the contagious distribution was larger than in the uniform one (P < 0.01). The ladybirds also consumed a larger number of aphids per day at high prey density than at low prey density when prey were distributed uniformly (P < 0.01). These results suggest that the ladybirds constantly consumed a small number of aphids in the uniform distribution, but the amount of prey consumed per day when predation occurred was larger, and prey consumption was much more variable, when the prey distribution was contagious.

3.3 Frequency of residence on the plants with aphids

The number of eggplants with aphids on which the ladybird was observed is shown in fig. 3. Ladybirds were more frequently observed on plants with high prey density than with low prey density (P < 0.01). Prey distribution also influenced the frequency of residence (P < 0.01), however, it was not surprising because initially there were nine times as many plants with aphids in the uniform treatment as in the contagious treatment. As the ladybirds came to a plant, they searched the whole plant. After they consumed an aphid, however, area-concentrated searching behaviour was observed.

4 Discussion

This study showed that prey density influenced prey consumption of the adult ladybirds, and that the frequency with which predation occurred was quite different between the prey distributions. The different predation patterns observed in the two spatial
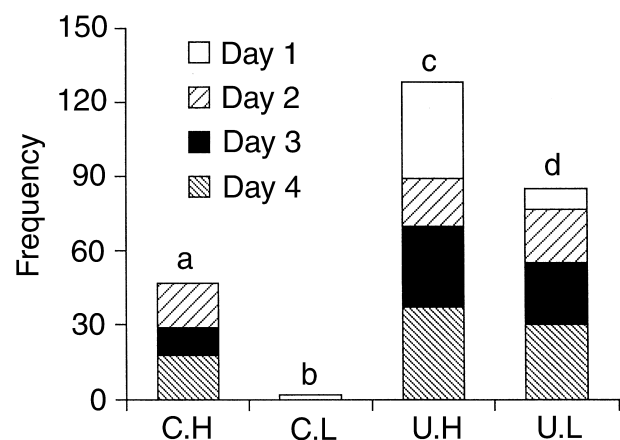
Table 2. *Numbers of days and of prey consumed per day when predation occurred at the cage during four successive experimental days with five replications*

Treatment	Numbers of	
	Prey consumed (mean ± SE)	Days when predation occurred
High contagious prey density	68.0 ± 17.1 a	7 a (35)
Low contagious prey density	11 abc	1 b (5)
High uniform prey density	23.1 ± 4.8 b	20 c (100)
Low uniform prey density	3.8 ± 0.6 c	19 c (95)

Means followed by the same letter are not significantly different in the number of prey consumed (Tukey's HSD test) and in the number of days (χ^2 test) between each treatment. Numbers in parentheses show percentages of predation occurred to 20 possible days of predation during four experimental days with five replications.

Fig. 3. *The number of eggplants with aphids on which the ladybird was observed. C, contagious; U, uniform, H, high density; L, low density. Frequencies followed by the different letter are significantly different in the number of ladybirds (χ^2-test) between each treatment*

distributions, of which prey consumption was much more variable in the contagious distribution, might be explained by the difference in prey encounter rate of the predator between the two distributions. As a higher prey encounter rate of the predator is predicted in the uniform distribution than in the contagious one because of a larger number of plants with aphids in a cage, a higher prey encounter rate in the uniform distribution results in a higher number of 'cage-days' during which predation occurred. Conversely, a small number of 'cage-days' with predation, but with high prey consumption per such 'cage-days' in the contagious distribution would be caused by the lower encounter rate but higher prey contagiousness.

The effect of spatial distribution on foraging efficiency of C. septempunctata larvae is changed by prey density; ladybird larvae consume a larger number of aphids at a low uniform prey density than at contagious prey density, but the opposite occurs at high prey density (MURAKAMI and TSUBAKI, 1984). Such a density-dependent change in foraging efficiency was also observed in the present study, suggesting that the effect of prey distribution on prey consumption is changed by prey density. In several species of ladybirds, area-concentrated prey searching behaviour after prey consumption is well known (BANKS, 1957; DIXON, 1959; NAKAMUTA, 1982, 1985; MURAKAMI and TSUBAKI, 1984); such was also observed in this study. The change in foraging efficiency with prey density from uniform to contagious prey distribution may result from this prey searching behaviour.

The effect of prey distribution on prey consumption by predators may vary with the predator's diet breadth. Even if a large number of prey occur on host plants in the field, small polyphagous predators such as mirids may consume a larger number of aphids in a uniform distribution than in a contagious one (CAPPUCCINO, 1987). However, this is unlikely for predatory ladybirds, as this prey consumption pattern in polyphagous predators appears to be caused by non-area-concentrated searching.

CAPPUCCINO (1987) shows that prey consumption by polyphagous insects is much more variable for a contagious prey distribution versus a uniform distribution; this was also observed in this study. These results suggest that high prey contagiousness leads to high variability in prey consumption irrespective of predator diet breath. Coccinella septempunctata adults can visually recognize a prey individual from a short distance (NAKAMUTA, 1984, 1985) and H. axyridis adult uses both olfactory and visual cues to detect an aphid (OBATA, 1986). In this study, even for the contagious distribution of prey at high density, no predation was observed on 65% of all experimental days, indicating that the prey-finding ability by these cues is probably limited in H. axyridis. Therefore, it seems that to find a host plant with prey individuals among several plants without prey is rather difficult for both oligophagous and polyphagous predators. This would lead to low foraging efficiency of these insects over large spatial scales.

The largest number of prey consumed in this study was 161 aphids over the total number of days of the experiment by nine predators in the contagious distribution with high prey density, or a mean number of prey consumed per day per capita estimated at 4.5 aphids, which is quite a small number. HUKUSIMA and OHWAKI (1972) report that H. axyridis adults consume much higher numbers of aphids in small cages. Harmonia axyridis adults spend 80% of the time in the field resting and walking, and little time is spent foraging (OBATA and JOHKI, 1990). Although a C. septempunctata female consumes over 100 aphids per day in a Petri dish (KAWAUCHI, 1990), field observation on prey consumption of C. septempunctata adults shows that the number of prey consumed is small, and that this beetle spends most time on other behaviour rather than prey foraging (SAKURATANI, personal communication). So, adult ladybirds may consume a small number of aphids when able to forage over a large spatial scale such as in the field. These results suggest that differences in the spatial scale influence foraging behaviour and prey consumption of ladybirds, and that experiments incorporating large spatial scale are needed to better understand the foraging behaviour of adult ladybirds.

Most adult ladybirds aggregate in the areas of high aphid density (MILLS, 1982; SAKURATANI et al., 1983; KAREIVA, 1984; OBATA and JOHKI, 1990; EVANS and YOUSSEF, 1992; IVES et al., 1993) and H. axyridis adults are more often observed on trees with abundant aphid colonies than on trees with low aphid density (OBATA and JOHKI, 1990). In the present study, when spatial distribution of prey held constant, the frequency of residence of ladybirds on experimental plants with aphids was higher at high aphid density than at low aphid density. This aggregation pattern of adult ladybirds can be explained by two different processes; one is the long residence of each ladybird on the plant, the other is the cumulative effect of many individuals which immigrate into and emigrate from the plant. IVES et al. (1993) show that individual adult ladybird response to aphid density is extremely weak but the cumulative effect of many individuals can produce strong population-level aggregation of ladybirds in the areas of high aphid density. So, the aggregation of adult ladybirds in areas with high aphid density often observed in the field may result from the cumulative effect of individual ladybirds' movements and responses to local prey density.

Differences in prey consumption patterns occur between the sexes in Adalia bipunctata (HEMPTINNE et al., 1996), and the time spent foraging in H. axyridis adults also differs between the sexes (OBATA and JOHKI, 1990). It is therefore necessary to conduct foraging experiments at large spatial scales with distinction of the sexes to understand adult behavior in ladybirds.

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