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Assessment of Patch Quality by Ladybirds: Role of Aphid and Plant Phenology

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Foraging theory indicates that aphid predators should lay their eggs early in the development of an aphid colony. Hoverflies appear to respond to cues associated with the age of an aphid colony in assessing its quality for oviposition. However, in the study reported here, ovipositing two-spot ladybirds did not respond differentially to two cues, in various combinations, associated with the age of aphid colonies on herbaceous plants: (a) age structure of the aphid colony and (b) the age of the plant. Thus, this aphid predator appears to be mainly using cues associated with the presence of conspecific larvae rather than those associated with aphids and/or plants when assessing patch quality.

KEY WORDS: ladybirds; *Adalia bipunctata*; patch quality; assessment.

INTRODUCTION

Some ladybirds exploit aphids, which are all patchily distributed. The numbers of aphids in each patch change in time, often dramatically, even in the absence of natural enemies (Dixon, 1997a). Ladybird larvae risk starvation if the aphids in the patch in which they have been oviposited disperse or become extinct before they can complete their development. In addition, their survival is dependent on the availability of prey in the immediate vicinity of the oviposition site because larvae have limited powers of dispersal. The decision by females where to oviposit is therefore of great importance

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because their fitness depends on their ability to determine which patches have the potential to sustain the development of their larvae. Foraging theory developed for invertebrate predators, and aphidophagous ladybirds in particular, indicates that if a female is to maximize its fitness, it should not oviposit in patches where prey are scarce and/or unlikely to remain abundant for long enough to support the growth of its larvae. It should therefore lay a few eggs early in the development of a patch (Kindlmann and Dixon, 1993).

It is well established that aphidophagous ladybirds lay most of their eggs over a relatively short period of time early in the development of aphid colonies. This period has been termed the egg window (Dixon, 1997b). The "window opens" when first-instar aphids are abundant enough for the vulnerable first-instar ladybird larvae to catch sufficient prey to sustain their development (Dixon, 1959). The "closing of the window" probably occurs when any further eggs laid in a patch are likely to be eaten by conspecific larvae (Hemptinne *et al.*, 1992; Doumbia *et al.*, 1998). Hoverflies similarly lay their eggs early in the development of an aphid patch (Kan, 1988a, b; Hemptinne *et al.*, 1993). They select the colonies by using visual cues, ovipositing in patches containing many young aphids and avoiding patches containing winged aphids, the presence of which indicates the colony will shortly disperse (Kan and Sasakawa, 1986). It is also possible that ladybirds similarly use cues emanating from the aphids or their host plant that could signal the "closing of the egg window" for reasons other than the risk of egg cannibalism. As a colony of aphids increases in abundance, its age structure changes and the host plant ages. The objective of this study is to determine whether cues associated with phenological changes in the prey population or plant are used as indicators of patch quality by ovipositing ladybirds.

MATERIAL AND METHODS

Ladybird Culture

Two-spot ladybirds, *Adalia bipunctata* (L.), were reared at $15 \pm 1°C$ and a photoperiod of 16 h light and 8 h darkness. Groups of approximately 20 males and 20 females were kept in 5-liter plastic boxes, which also contained a piece of corrugated filter paper to increase the surface area. Every other day the ladybirds were fed an excess of pea aphids, *Acyrthosiphon pisum* (Harris). On that occasion, a section of stem of broad bean, *Vicia faba* L., was put in each of the rearing boxes to provide a source of humidity and to keep the aphids alive as long as possible. Once a week the ladybirds were transferred to clean containers to stimulate egg-laying.

All the adults were reared from the egg stage in the laboratory. The eggs were collected every day and incubated in 175-cm^3 boxes under the same day-length and temperature conditions as experienced by the adults. After hatching, the larvae were also fed an excess of pea aphids. In order to reduce the risk of cannibalism, the number of larvae per box never exceeded 15. Prepupae were transferred to a $20 \pm 1°C$ cabinet to reduce their developmental time. On emergence adults were placed in groups in boxes as described above.

Morphological Characteristics of the Instars of the Pea Aphid

In order to set up pea aphid populations of different age structures, it was necessary to be able to recognize the different instars of the aphid. To do this, a freshly cut broad bean leaf (*V. faba*) with its petiole wrapped in a piece of wet cotton wool was placed in a 9-cm-diameter Petri dish. An apterous adult female of the pea aphid was taken from the stock culture and put on the leaf for 24 h at $21 \pm 1°C$ and a photoperiod of 16 h light and 8 h darkness. The adult aphid was then removed and the offspring born during that interval were allowed to mature. When the bean leaf showed signs of wilting, it was replaced and the aphids gently transferred to a new leaf using a paintbrush.

The length of the antennae and of the body, from the base of the antennae to the tip of the cauda, of each aphid were measured daily under a binocular microscope using a graticule eye-piece. The state of the segmentation of the abdomen was also observed. These characters are known to vary with aphid age (Heie, 1995) and were chosen because they are easy to observe and record. The days on which the aphids molted were also recorded. There were 10 replicates of five aphids.

Age Structure of Pea Aphid Colonies

Two pea plants (*Pisum sativum* L. cv Eminant petit provencal) were individually grown in square pots ($10.5 \times 10.5 \times 12.5$ cm) filled with a commercial compost. They were each kept under a cylindrical cage (diameter 25 cm, height 50 cm) consisting of a metal frame covered by muslin, in a greenhouse where the minimum temperature was always at least 25°C. There was, however, no regulation of the maximum temperature. Supplementary lighting operated for 16 h per day.

When the pea plants produced their sixth leaf, they were each infested with an adult apterous female aphid from the stock culture, which the day before was placed individually on a pea leaf in a 5-cm-diameter Petri dish to check that it was producing offspring. Every day, the aphids were counted and their instar recorded. The numbers in each instar each day were summed from the start of the infestation to the peak in abundance and for the period after the peak. The first total number was used to calculate the average proportion of the various instars in the populations prior to the peak, which was assumed to be typical of a young aphid colony. Similar calculations were made with the second total for the period after the peak, which was assumed to be typical of an old aphid colony.

The Effect of Plant Age and Aphid Age Structure on Egg Laying by *A. bipunctata*

Eighty pea plants were grown as outlined above. Two weeks after germination, 40 of these young pea plants were infested with aphids; 20 with 100 aphids with the age structure of a young aphid colony and 20 with 100 aphids with an age structure of an old colony. The remaining 40 pea plants started to flower when approximately 1 month old. These were the old plants and were infested with aphids similarly to that described for the young plants.

The aphids on the two ages of plants were allowed to settle for 24 h before a mature female of *A. bipunctata* was placed on each plant and the numbers of eggs it laid were recorded after 3 h. The ladybirds were taken from the stock culture just before the start of the experiment and were between 10 and 30 days old.

This experiment was done in a greenhouse from the beginning of April to mid May. The numbers of eggs laid in each treatment were square-root-transformed, to meet the requirements of normality and homoscedasticity, and then compared by means of a two-way ANOVA.

RESULTS

Morphological Characteristics of the Instars of the Pea Aphid

The instars of the pea aphid can be separated on the basis of their body length, the length of their antennae relative to that of their body, and the more or less marked segmentation of the abdomen (Table I). For the purpose of this study, first- and second-instar aphids are referred to as small, and the third- and fourth-instar aphids as large.

Table I. Mean Body Length and Two Morphological Characteristics of the Four Nymphal Instars of the Pea Aphid, *Acyrthosiphon pisum* ($n = 50$)

	Instar			
Characteristic[a]	First	Second	Third	Fourth
Mean length, (mm) (SEM)	1.3 (0.0)	1.6 (0.8)	2.0 (0.9)	2.4 (1.1)
Abdomen	Weakly segmented		Distinctly segmented	
Antennae	Equal to body length		Greater than body length	

[a] SEM, Standard error of the mean.

Age Structure of Pea Aphid Colonies

The numbers and percentages of the different instars of the pea aphid were followed on the two plants. On one plant the aphids reached peak abundance on day 8 and the colony lasted for 15 days. On the other plant the peak occurred after 6 days and the colony survived for 10 days. The relatively high temperature in the greenhouse determined the short period for which the colonies lasted. Before the peak in abundance, i.e., in the young colonies, there were significantly more small larvae and fewer adult aphids than after the peak, i.e., in old colonies (Table II, $\chi^2 = 224.27$; 2 df, $P < 0.001$). The percentages of small, large, and adult aphids recorded here (Table II) were used in the next experiment to create young or old colonies of aphids with individuals collected from the stock culture.

The Effect of Plant Age and Aphid Age Structure on Egg Laying by *A. bipunctata*

The age of the plants and the structure of aphid colonies did not affect the number of females laying eggs (Table III: $\chi^2 = 0.21$, 3 df, $P > 0.05$).

Table II. Mean Percentages of Small, Large, and Adult Aphids in Young and Old Colonies of the Pea Aphid, *Acyrthosiphon pisum*

	Aphid/instar		
Age of aphid colony	Small (1st + 2nd instars)	Large (3rd + 4th instars)	Adult (winged + unwinged)
Young	79.2	18.4	2.4
Old	10.3	57.8	31.9

Table III. Mean Numbers of Eggs Laid by the Ladybird, *Adalia bipunctata*, on Young and Old Pea Plants Infested with Colonies of the Pea Aphid, *Acyrthosiphon pisum*, Which Had Age Structures Characteristic of Young and Old Colonies, Respectively

	Aphid colony[a]					
	Young			Old		
Plant	n_1	n_2	$\bar{X}$(SEM)	n_1	n_2	$\bar{X}$(SEM)
Young	20	13	5.1 (1.2)	20	12	4.9 (1.2)
Old	20	13	3.6 (0.8)	20	15	8.7 (2.5)

[a] n_1, Number of replicates; n_2, number of females laying eggs; SEM, standard error of the mean.

Ladybirds laid similar numbers of eggs in the four treatments (Tables III and IV), and 70% of their eggs were laid on the plants. That is, these results indicate that the two-spot ladybird did not use the age of the plant and/or the age structure of the aphid colonies as a cue for oviposition.

DISCUSSION

The elegant experiments done by Kan (1988a, b) and Kan and Sasakawa (1986), in which they experimentally manipulated the apparent age structure of aphid colonies by removing and sticking wings on aphids and dummies of aphids clearly indicate that hoverflies visually scan aphid colonies and avoid ovipositing in those that contain a high proportion of winged individuals. The presence of winged individuals is a good indicator of imminent dispersal and disappearance of the colony. Hoverfly females behave as if they were "buying future" for their larvae, using the expression that Kan and Sasakawa (1986) borrowed from economics to describe this phenomenon. Although in terms of compound eyes and gustatory and olfactory receptors

Table IV. Analysis of the Effect of Age of Plant and Age Structure of Aphid Colonies on the Numbers of Eggs Laid[a]

Source of variation	Degrees of freedom	Mean square	F
Age of plants	1	0.394	0.17 NS
Age structure of aphid colonies	1	1.132	0.50 NS
Interaction	1	2.259	0.76 NS
Residuals	76	2.960	

[a] NS, Not significant.

ladybirds and hoverflies appear to be similarly endowed, there is no evidence from this study that ovipositing two-spot ladybirds respond to cues associated with either aphid or plant phenology. A previous study on *Coccinella septempunctata* L. indicated that foliage heavily contaminated with aphid honeydew and molt skins, as often accumulate around old aphid colonies, had only a weak deterrent effect on ovipositing females (Hemptinne *et al.*, 1993). That is, relative to the very strong response to the deterrent effect of larval tracks shown by ovipositing *Adalia bipunctata* and *Coccinella septempunctata* (Doumbia *et al.*, 1998), other cues indicating the age of an aphid patch, and therefore the time it is likely to last, appear to be very weak or to have no effect.

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