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Assessment of patch quality by ladybirds: role of larval tracks

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Abstract Gravid females of the two-spot ladybird, *Adalia bipunctata* (L.), were deterred from ovipositing when kept in petri dishes that had previously contained conspecific larvae but not conspecific adults, or the larvae of another two species of ladybird, *Adalia decempunctata* (L.) and *Coccinella septempunctata* L. The deterrent effect was density dependent and mediated via a chloroform-soluble contact pheromone present in the larval tracks. Similarly, gravid females of *C. septempunctata* were deterred from ovipositing by conspecific larval tracks and chloroform extracts of these tracks, but not by the tracks or extracts of tracks of *A. bipunctata* larvae. That is, in ladybirds the larvae produce a species-specific oviposition-deterrence pheromone. In the field, the incidence of egg cannibalism in ladybirds increases very rapidly with the density of conspecific eggs or larvae per unit area. Thus, in responding to the species-specific oviposition-deterrence pheromone female ladybirds reduce the risk of their eggs being eaten and spread their offspring more equally between patches.

Key words Cannibalism · Coccinellidae · Larval tracks · Oviposition-deterrence pheromone · Patch quality

Introduction

It is of practical and theoretical interest to understand the foraging behaviour of insect predators. Most optimal foraging theory has been developed for vertebrates (e.g. Stephens and Krebs 1986) and is not directly applicable to invertebrate predators. Not only is it highly

unlikely that adult invertebrate predators have the level of omniscience necessary to forage optimally but their immature stages mostly forage for food independently of their parents. Foraging theory developed for invertebrate predators, and ladybirds in particular, indicates that if the females are to maximize their fitness they should not oviposit in patches where prey are scarce and/or unlikely to remain abundant long enough to sustain the development of their larvae (Kindlmann and Dixon 1993).

The survival of the larvae of ladybirds is dependent on the availability of prey in the immediate vicinity of the oviposition site because they have limited powers of dispersal. Some ladybirds exploit aphids, which are all patchily distributed. The patches consist of clumps of food or simply heterogeneities in the prey distribution (Stephens and Krebs 1986). The numbers of aphids in each patch change in time, often dramatically, even in the absence of natural enemies (Dixon 1985). Ladybird larvae risk starvation if the aphids in the patch they have been oviposited in are too sparse or become sparse or extinct before they can complete their development. In addition, the period for which a patch can sustain larvae is dependent on the number of larvae in the patch. Larval survival is therefore likely to be low if too many eggs are laid or they are laid too late, i.e., when aphid numbers are declining. The decision by females to lay eggs or to refrain from ovipositing is of great importance because their fitness depends on their ability to assess the quality of patches in terms of their potential to sustain the development of their larvae. One immediate threat to the survival of their offspring is egg cannibalism by larvae already present in a patch. In the field, the incidence of egg cannibalism increases very rapidly with the number of larvae in a patch (Mills 1982; Osawa 1989). Therefore, if they are to maximize their fitness these predators should lay a few eggs early in the development of a patch (Kindlmann and Dixon 1993).

What evidence is there that invertebrate predators distribute their offspring in the way theory predicts and how do they do it? Field and laboratory studies indicate

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that ladybirds tend to lay eggs where there are sufficient aphids for the survival of their first-instar larvae (Dixon 1959; Honek 1978; Mills 1979; Wratten 1973) and mainly early in the development of a prey patch. Laboratory studies also show that ladybirds avoid ovipositing in the presence of conspecific larvae (Hemptinne and Dixon 1991; Hemptinne et al. 1992). The co-cicidophagous ladybird *Cryptolaemus montrouzieri* Muls. and the aphidophagous chrysopid, *Chrysopa oculata* Say are similarly reluctant to oviposit in the presence of conspecific larvae (Merlin et al. 1996a, b; Ruzicka 1994). In the latter case this is due to the presence of an oviposition deterring pheromone in the tracks left by the larvae (Ruzicka 1994). In one case the deterrent factor is known to act at a distance. The predatory mite, *Phytoseiulus persimilis* Athias-Henriot, at least in the laboratory, responds to volatiles produced by conspecifics and so avoids patches of prey already being exploited (Janssen et al. 1997). Thus, in common with phytophagous insects and insect parasitoids, which have been more extensively studied in this respect (e.g. Price 1970; Prokopy 1972, 1981; Rothschild and Schoonhoven 1977; van Lenteren 1981; Janssen et al. 1995), ovipositing predatory insects also respond to cues indicating that a patch is already being exploited by conspecifics.

A good biological control agent is one that stabilizes the abundance of the pest well below the economic threshold (Murdoch 1990; Murdoch et al. 1985). To achieve this the natural enemy needs to show a strong aggregative response to high densities of prey (Beddington et al. 1978; Hassell 1978; Begon et al. 1996). However, the numerical response shown by *A. bipunctata* to increasing prey density is weakened by its tendency to avoid ovipositing in patches already exploited by conspecific larvae (Hemptinne et al. 1992). For this reason natural populations of ladybirds are thought to have been unsuccessful when used as biological control agents against aphids (Dixon et al. 1995). Therefore, it is important to understand how ladybirds assess the quality of patches of prey.

In this paper, we present results of experiments exploring the nature of the cues that deter two species of aphidophagous ladybirds (*Adalia bipunctata* (L.) and *Coccinella septempunctata* L.) from ovipositing in prey patches already exploited by ladybirds.

Materials and methods

Experimental animals

The ladybirds were fed on pea aphids, *Acyrtosiphon pisum* (Harris), which were reared on young broad bean plants (*Vicia faba* L.) grown in a mixture of perlite and vermiculite (50:50) at 20°C and a 16-h photoperiod, and watered as required. The period from germination of the beans to their replacement with fresh plants was approximately one month. Prior to experiments, female ladybirds were fed an excess of a mixture of aphids of different instars and their egg-laying rate monitored for 4 days. The females of *A. bipunctata* obtained from a stock culture, were of unknown age, tended to lay eggs on alternate days, and were designated type A

females. In an attempt to reduce the variability of the results after the first experiment, more attention was paid to the quality of the females. They were reared in isolation, were between 15 and 25 days old at the beginning of the experiment and had been recently mated. They were designated type B females. Five days before each test, the number of eggs laid by each female was counted daily. Only those producing at least one clutch of eggs per day were selected for the experiments. To control for the variability between days, only one replicate of each treatment along with the corresponding control were realized each day. Females of *C. septempunctata* collected from the field after emerging from hibernation, kept at 20°C, and offered an abundance of aphids quickly started reproducing and tended to lay eggs daily. All experiments were done at 20°C and a light intensity of 414 lux.

Statistical analyses were performed with Systat (Wilkinson et al. 1992).

Oviposition by *A. bipunctata*

The effect of conspecific larval tracks

Fifteen first-, second-, third- or fourth-instar larvae were supplied with an excess of a mixture of different instars of the pea aphid in a 9-cm petri dish, the base of which was covered with filter paper. After 24 h the larvae and all aphid material were carefully removed. A single type A female was then placed in each dish at 08 00 hours with an excess of aphids, and the number of eggs it had laid recorded 3 h later. The experiment was repeated 30 times for each larval instar and for the controls. The controls were run in parallel with the experimental beetles and consisted of 30 females kept individually in petri dishes that had contained a similar number of aphids but no larvae over the previous 24 h. The results of the experiments were analysed by mean of a three-way ANOVA with two fixed factors (larval instars, presence or absence of larvae) and a random factor (days). The proportions of females ovipositing were arcsine transformed and compared by a test based on the normal distribution (Dagnelie 1975).

To determine whether the deterrent effect was dependent on the number of larvae the following experiment was done. The same general procedure as above was followed but 1, 5 or 10 fourth-instar larvae were placed in each petri dish with an excess of aphids for 24 h. Each treatment was replicated 21 times along with the corresponding number of controls. Type B females were used. As the numbers of eggs laid in the three controls were not significantly different (ANOVA: $F = 1.16$, 2, 60 *df*, $P > 0.05$), the controls were pooled together to become the treatment '0 fourth-instar larva'. The numbers of eggs laid in 3 h were recorded and compared by a two-way ANOVA with one fixed factor (density of larvae) and a random factor (days). Pairwise comparisons of means with unequal numbers of replications were performed to identify whether results differed between treatments (Kramer 1956; Hartler 1960).

Each female in the above experiment was also observed on ten occasions at 90-s intervals during the first, third, fifth, seventh, ninth and eleventh 15-min interval from the start of the experiment. That is, each female was observed 60 times over the 3-h period and whether she was laying eggs noted. The number of times observed egg laying and the proportions of females laying eggs in the control and the experimental treatments were arcsine transformed and compared by a test based on the normal distribution (Dagnelie 1975).

The effect of conspecific adult tracks

Fifteen male or female *A. bipunctata* beetles were kept with an excess of a mixture of different instars of pea aphid for 24 h in a 9-cm petri dish, the base of which was covered with filter paper. After the adults and aphid material were removed, a single young gravid type B female of the same species was placed in each dish with an excess of aphids and the number of eggs it laid in 3 h recorded. This was repeated 30 times for each sex and for the

control, which consisted of petri dishes previously only occupied by aphids. The numbers of eggs laid in 3 h were compared by a two-way ANOVA with one fixed factor (presence of conspecifics) and a random factor (days).

The effect of chloroform extract of conspecific larval tracks

Fifteen fourth-instar larvae of *A. bipunctata* were kept with aphids in a 50-ml glass vial for 24h, after which the larvae and aphids were removed and the inside of the vial rinsed with 1 ml of chloroform for 1 min. The chloroform extract was applied to a 9-cm-diameter filter paper and the chloroform evaporated off in a fume cupboard for 20 min. Chloroform was used because it is a good general solvent. The filter paper was subsequently placed in a 9-cm petri dish. A gravid type B female and an excess of aphids were added to the dish at 08 00 hours and after 3 h the number of eggs laid was recorded. This was repeated 30 times, and 30 times for the control, which had no coccinellid larvae but was otherwise treated similarly. The results were analysed by mean of a two-way ANOVA (fixed factor: presence or absence of the extract; random factor: days).

The effect of odour of conspecific larvae

To determine whether the odour of larvae deterred adults from ovipositing, the following experimental procedure was adopted. Air was pumped (17 l/h) first through water to wash and humidify it, then through a carbon filter and finally through a 50-ml conical flask, which contained 15 fourth-instar larvae with an excess of aphids before passing through a 9-cm petri dish lined with filter paper and containing one gravid type B female and an excess of aphids. The numbers of eggs laid in 3 h was recorded. This was repeated 21 times and 21 times for the control, which had no larvae in the conical flask but was otherwise similar. The results were analysed by mean of a two-way ANOVA (fixed factor: presence or absence of the odour; random factor: days).

The effect of larval tracks of A. decempunctata and C. septempunctata

To determine whether the larvae of other species of ladybird deterred a ladybird from ovipositing a similar experiment to that outlined above (the effect of conspecific larval tracks) was done. However, 15 fourth-instar larvae of *A. decempunctata* or *C. septempunctata* were used instead of conspecific larvae. The test animals were type B females and each experiment was replicated 15 times along with the corresponding controls. For each species of ladybird, the numbers of eggs laid were compared by means of a two-way ANOVA (fixed factor: presence or absence of ladybirds; random factor: days).

Oviposition by C. septempunctata

The effect of conspecific and heterospecific larval tracks

Ten 4- to 7-day-old larvae (third or fourth instar) of *C. septempunctata* were placed for 24 h in a 9-cm petri dish the base of which was lined with filter paper. To prevent cannibalism the larvae

were periodically removed and fed a few aphids and then returned to the dish. After 24 h the piece of filter paper was placed at one end of a plastic box (11.6 × 17.5 × 6 cm), at the other end of which was a clean piece of filter paper. Eight females and two males were added to the box with an excess of aphids. Every 2 h for 16 h, the number of clutches of eggs laid on the two pieces (clean/contaminated) of filter paper were recorded. The experiment was repeated ten times. Results were analysed using a test of homogeneity followed by a χ^2 test on the total number of clutches of eggs laid on the two substrates. In a similar experiment to the above, *A. bipunctata* larvae were used instead of *C. septempunctata*. This was replicated six times.

The effect of chloroform extract of conspecific and heterospecific larval tracks

The above experiment was repeated but with filter paper contaminated with a chloroform extract of the larval tracks. Ten four to seven day old larvae were placed into a 25 ml flask for 12 h, after which the inside of the flask was rinsed with 2 ml of chloroform. The chloroform solution was transferred to filter paper and the chloroform evaporated off in a fume cupboard. The experiment with *C. septempunctata* was replicated ten times and that with *A. bipunctata* six times.

Results

Oviposition by A. bipunctata

The effect of conspecific larval tracks

Gravid females of *A. bipunctata* were deterred from ovipositing, both in terms of the total number of eggs laid ($F = 38.95$, 1, 29 *df*, $P = 0.000$) and the number of females ovipositing, when kept in petri dishes that had previously contained conspecific larvae. A similar level of deterrence was observed for all larval instars (Table 1). That is, the presence of conspecific larval tracks of all four instars deterred gravid females of *A. bipunctata* from ovipositing.

The deterrent effect of the larval tracks on oviposition displayed a density-dependent trend: $y = (13.0 \pm 1.0) - (1.1 \pm 0.2)x$; where y stands for the number of eggs laid and x for the density of larvae ($r = 0.42$, $F = 26.36$, 1, 124 *df*, $P = 0.000$). When one larva had previously been kept in the petri dishes, females laid fewer but not significantly fewer eggs than the controls (Table 2) but spent significantly less time ovipositing than the control females (Table 2). The reduction in the numbers of eggs laid relative to the controls was pro-

Table 1 The mean numbers of eggs laid and the numbers of females of *Adalia bipunctata* ovipositing in petri dishes that had previously contained different instars of conspecific larvae for 24 h and in clean petri dishes (control). Means followed by the same letter are not significantly different ($P = 0.001$)

| | Larval instars | | | | |
|---|----------------|-------------|-------------|-------------|-------------|
| | First | Second | Third | Fourth | Control |
| No. of replicates | 30 | 30 | 30 | 30 | 120 |
| Mean no. of eggs (SEM) | 2.4 (1.2) a | 3.1 (1.5) a | 2.9 (1.4) a | 1.9 (1.3) a | 8.7 (0.9) b |
| % Females ovipositing | 13.3 | 13.3 | 20.0 | 6.7 | 49.2 |
| Tests of proportion relative to the control | 3.6766*** | 3.6766*** | 2.8293*** | 4.7041*** | |

For the tests of proportions, *** $P < 0.001$

Table 2 The numbers of eggs laid by females of *Adalia bipunctata*, the numbers of females that laid eggs and the number of times each female was observed ovipositing in petri dishes that had previously contained 0, 1, 5 or 10 fourth instar conspecific larvae for 24 h. Means followed by the same letter are not significantly different ($P = 0.001$)

| | Number of larvae | | | |
|--|------------------|--------------|--------------|-------------|
| | 0 | 1 | 5 | 10 |
| No. of replicates | 63 | 21 | 21 | 21 |
| Average number of eggs (SEM) | 14.0 (1.1) a | 9.5 (2.6) ab | 6.3 (1.9) bc | 2.7 (1.3) c |
| % Females ovipositing | 87.3 | 42.9 | 38.1 | 23.8 |
| Tests of proportion relative to '0 larva': | | 4.5706*** | 4.9889*** | 6.1933*** |
| % Time observed ovipositing | 10.2 | 5.8 | 3.2 | 1.7 |
| Tests of proportion relative to '0 larva' | | 2.6954*** | 4.2585*** | 5.2369*** |

For the tests of proportions, *** $P < 0.001$

gressively greater when five and ten larvae had contaminated the petri dishes. In these cases, the differences in the numbers of eggs laid by the control and experimental females were significant (Table 2) as were the proportions of females that laid eggs and the proportions that were seen ovipositing (Table 2).

Conspecific adult tracks

Previous presence of conspecific adults, males or females, unlike that of larvae did not deter oviposition by *A. bipunctata* (Table 3).

Extracts of conspecific larval tracks

The chloroform extract of the tracks of larvae had a very marked deterrent effect on oviposition by *A. bipunctata* (Table 4). That is, the oviposition deterrent is a chloro-

Table 3 The average number of eggs laid in 3 h by *A. bipunctata* in petri dishes that had previously contained conspecific males and females for 24 h relative to the average number laid in clean petri dishes (figure in parentheses is the standard error. ANOVA: $F = 0.85$, $df = 2, 58$; $P = 0.433$, NS)

| Treatment | No. of replicates | Average number of eggs |
|-----------|-------------------|------------------------|
| Control | 30 | 15.7 (2.0) |
| Male | 30 | 17.2 (1.7) |
| Female | 30 | 14.0 (1.7) |

Table 4 The average number of eggs laid in 3 h by *A. bipunctata* in petri dishes that contained filter paper treated with a chloroform extract of conspecific larval tracks and in control petri dishes (figure in parentheses is the standard error; ANOVA: $F = 9.617$, $1, 29$ df , $P = 0.004$)

| Treatment | No. of replicates | Average number of eggs |
|-------------------------|-------------------|------------------------|
| Extract of larval track | 30 | 7.5 (1.9) |
| Control | 30 | 15.5 (1.6) |

roform soluble chemical(s) present in the tracks left by larvae.

Odour of conspecific larvae

The odour of conspecific larvae did not deter *A. bipunctata* from ovipositing (Table 5).

Tracks of the larvae of C. septempunctata and A. decempunctata

In contrast to the effect of conspecific larval tracks, those of *C. septempunctata* and *A. decempunctata* did not affect oviposition by *A. bipunctata* (Table 6). This indicates that the deterrent response is possibly not general to the presence of larvae of all species of ladybirds but specific to conspecific larvae.

Table 5 The average number of eggs laid in 3 h by *A. bipunctata* in petri dishes flushed through with air that has passed over conspecific larvae and with clean air (figure in parentheses is the standard error; ANOVA: $F = 0.072$, $df = 1, 20$, $P = 0.791$)

| Treatment | No. of replicates | Average number of eggs |
|-----------------|-------------------|------------------------|
| Odour of larvae | 21 | 17.3 (1.8) |
| Control | 21 | 16.5 (2.3) |

Table 6 The average number of eggs laid in 3 h by *A. bipunctata* in petri dishes that had previously contained **A** larvae of *Coccinella septempunctata* or **B** larvae of *A. decempunctata* for 24 h, relative to the number laid in clean (control) petri dishes (figure in parentheses is the standard error; ANOVA_{*C. septempunctata*}: $F = 0.014$, $df = 1, 14$, $P = 0.908$, NS; ANOVA_{*A. decempunctata*}: $F = 0.536$, $df = 1, 14$, $P = 0.476$, NS)

| Treatment | No. of replicates | Average number of eggs laid |
|---------------------------------|-------------------|-----------------------------|
| A | | |
| <i>C. Septempunctata</i> larvae | 15 | 19.3 (2.0) |
| Control | 15 | 19.6 (2.0) |
| B | | |
| <i>A. decempunctata</i> larvae | 15 | 15.1 (3.5) |
| Control | 15 | 18.3 (1.9) |

Table 7 The numbers of clusters of eggs laid by *C. septempunctata* on filter paper that had **A** previously been walked on by conspecific larvae or treated with a chloroform extract of the tracks left by conspecific larvae (contaminated) and on clean filter paper (control) or **B** on similarly treated filter paper but using the larvae of *A. bipunctata* (***) $P < 0.001$)

| Treatment | No. of replicates | Contaminated | Control | χ^2 |
|-------------------|-------------------|--------------|---------|----------|
| A | | | | |
| Larval tracks | 10 | 4 | 46 | 35.3*** |
| Extract of tracks | 10 | 11 | 65 | 38.4*** |
| B | | | | |
| Larval tracks | 6 | 16 | 14 | 0.13 NS |
| Extract of tracks | 6 | 21 | 23 | 0.91 NS |

The effect of conspecific and heterospecific larval tracks on oviposition by *C. septempunctata*

As in *A. bipunctata* the previous presence of conspecific but not heterospecific larvae had a marked effect on the number of egg clusters laid by *C. septempunctata* (Table 7A). Similarly, an extract of conspecific but not heterospecific larval tracks deterred adults from ovipositing (Table 7B). That is, females of *C. septempunctata*, like those of *A. bipunctata*, avoid laying eggs on substrates that had previously been traversed by conspecific larvae, but did not respond to the tracks of heterospecific larvae.

Discussion

This study confirms the finding of Hemptinne et al. (1992) that aphidophagous ladybirds are reluctant to oviposit in the presence of conspecific larvae: females reacted to physical encounters with conspecific larvae but did not respond to contacts with a closely related species. The results presented here indicate the adults do not need an encounter with larvae to refrain from ovipositing. They are very sensitive to a chemical cue present in the tracks left by larvae. The molecules that modify the oviposition behaviour of female ladybirds are soluble in chloroform but are not volatile as females did not respond to the "odour" of conspecific.

It is now well established that females of insects belonging to the third trophic level carefully select their oviposition sites and so maximize their fitness. Some assessment of patch quality is critical because it determines the survival and growth rate of the offspring. Selection will favour females that avoid ovipositing where competitors threaten the survival of their offspring. Females do this mainly by responding to semiochemicals released by conspecific competitors. For example parasitoids are sensitive to volatiles signalling the previous or actual presence of conspecifics or enemies (Price 1970; Höller et al. 1994; Janssen et al. 1995) and several aphidophagous or coccidophagous predators respond to non-volatile molecules in the tracks left by conspecific larvae (Hemptinne et al. 1993; Ruzicka

1994; Merlin et al. 1996b). By responding in this way females greatly reduce the time needed to assess the quality of patches and consequently enhance the probability of discovering suitable oviposition sites.

Confining adults in petri dishes that had previously contained different numbers of larvae revealed that egg laying rates are related to the quantity of the oviposition deterring pheromone present. In the field, the incidence of egg cannibalism in ladybirds increases very rapidly with the egg or larval density per unit area (Mills 1982). In the laboratory, egg cannibalism is inversely related to the abundance of aphids (Agarwala and Dixon 1992) and gravid females are reluctant to lay eggs in the absence of aphids, i.e. the presence of aphids stimulates oviposition (Evans and Dixon 1986). Thus, in assessing a patch of prey, ladybirds possibly monitor both the concentration of the oviposition-detering pheromone and the stimulatory cues associated with aphids and rely on the relative concentrations of these stimuli to assess the risk of their eggs being eaten. In addition, the decision to oviposit is also likely to be influenced by the transit time between patches and the general quality of patches of prey (Stephens and Krebs 1986).

The avoidance displayed by females is accompanied by changes in their behaviour. They become more agitated and spend a greater proportion of their time walking rapidly, which would result in them leaving the patch (Price 1970; Hemptinne et al. 1992). Price (1970) thought that this change in behaviour could result in a more even distribution of individuals between patches, approaching that of an ideal free distribution (Janssen et al. 1997). The latter, however, is not necessarily realised by foraging insects as it depends on individuals being able to assess the average density of a resource, its rate of depletion and the distance between patches (Bernstein et al. 1991; Kacelnik et al. 1992). Ladybird beetles have a developmental time that is similar to the average life span of an aphid colony. It does not make sense for ladybirds to lay eggs in old aphid colonies as their offspring will not be able to complete their development. Therefore, there is a great selective advantage in being able to detect aphid colonies in the early stage of their development (Kindlmann and Dixon 1993). Field data show that ladybirds usually lay most of their eggs well before their resource peaks in abundance (Hemptinne et al. 1992). This results in an inverse numerical response and severely constrains the potential effectiveness of ladybirds as biocontrol agents of aphids (Dixon et al. 1995).

It is interesting to speculate why adults respond only to conspecific larvae. It is likely that each species of ladybird is associated mainly with one particular habitat (*cf* Honek 1985). That is, overall it is more likely to meet individuals of its own species than of other species, and particularly so in its preferred habitat. If this is the case then the greatest threat to survival is other individuals of its own species.

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