Oviposition responses to patch quality in the larch ladybird *Aphidecta obliterata* (Coleoptera: Coccinellidae): effects of aphid density, and con- and heterospecific tracks

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Abstract

The effects and persistence of oviposition-deterring semiochemical cues from conspecific and heterospecific larval tracks on the oviposition rate of *Aphidecta obliterata* (Linnaeus) females were investigated. In addition, the effects of varying aphid prey density were considered and also whether any resulting response originated from differential nutritional status of females and/or due to aphid odour stimuli. The existence of oviposition responses to conspecific egg chemicals was also considered. Gravid *A. obliterata* females were deterred from oviposition by conspecific larval tracks and the effect was density dependent. Females actively avoided searching in these contaminated areas. Tracks induced a significant effect on oviposition for up to three days. Heterospecific tracks of the coccinellid *Adalia bipunctata* (Fabricius) or the chrysopid *Chrysoperla carnea* (Stephens) did not induce any oviposition response in *A. obliterata* females. Increasing aphid density induced increased oviposition rate in *A. obliterata* females. Nutritional status of females was an important factor in the relationship between aphid density and oviposition rate, but aphid associated cues (odours) were not. There was an inhibitory effect of extracts of conspecific egg-surface chemicals on oviposition by *A. obliterata* females. In the field, cannibalism, competition and limited food availability represent the major threats to egg and larval survival. Patch quality assessment mechanisms enable females to lay eggs at sites where offspring survival is maximized. Oviposition-deterring semiochemicals tend to promote more even distribution of predators over prey patches.

Keywords: *Aphidecta obliterata*, *Adalia bipunctata*, *Chrysoperla carnea*, ladybirds, oviposition, prey density, semiochemicals, patch quality

Introduction

The larch ladybird *Aphidecta obliterata* (Linnaeus) (Coleoptera: Coccinellidae) is an important natural enemy of the green spruce aphid, *Elatobium abietinum* (Walker)

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(Hemiptera: Aphididae), a serious pest of Sitka spruce (*Picea sitchensis* Bong. (Carr.)), Britain's main commercially grown tree (Carter & Halldorson, 1998). *Aphidecta obliterata* has been used in a biological control programme in Germany to control *Adelges piceae* (Ratzeburg) (Hemiptera: Adelgidae), a pest of *Abies* spp. (Hodek, 1973). The foraging behaviour of aphidophagous coccinellids (Dixon, 1959; Wratten, 1973; Mills, 1982; Carter & Dixon, 1984) and the interactions between larvae and adults (Hassell, 1978; Hemptinne *et al.*, 1992) have been much studied, but relatively little attention

has been paid to semiochemical spacing of aphidophagous predators over prey patches of different quality (Evans & Dixon, 1986).

Potential oviposition sites differ in the probability of offspring survival due to spatial variation in prey, predator and competitor abundance. Egg-laying females obtain different fitness returns depending on oviposition site, setting up selection pressures facilitating the evolution of patch quality assessment mechanisms by females. These mechanisms involve receiving appropriate stimulation from mechano- and chemoreceptors to induce oviposition (Chapman, 1998). Many species of aphidophagous predators, from three insect orders: Neuroptera, Coleoptera and Diptera, have been shown to possess larvae whose tracks contain semiochemicals acting to deter oviposition by conspecific females. Coccinellids studied include *Adalia bipunctata* (Fabricius) (Doumbia *et al*., 1998), *Coccinella septempunctata* (Linnaeus) (Růžička 1997; Doumbia *et al*., 1998), *Cycloneda limbifer* (Casey), *Semiadalia undecimnotata* (Schneider) (Růžička, 2001) and *Harmonia axyridis* (Pallas) (Yasuda *et al*., 2000).

Coccinellid larvae may deposit oviposition-deterring semiochemicals (ODS) from the tip of their abdomen, which they use as a pseudopod (Růžička, 2001). The chemicals are possibly detected by adults using the maxillary palpi (Růžička, 2003). Oviposition-deterring semiochemicals have been shown to be soluble in chloroform (Růžička, 1994; Doumbia *et al*., 1998) and also water (Růžička, 1994; Růžička & Havelka, 1998). However, this conflicts with evidence that they comprise mixtures of (hydrophobic) alkanes similar to those found on the elytra of the adults and on the surface of conspecific eggs (Hemptinne *et al*., 1998, 2001). The alkanes on elytra are used in mate recognition (Hemptinne *et al*., 2000c), and those on the surface of eggs may be important in chemical defence from intraguild predation (Agarwala & Yasuda, 2001). A similar mixture of alkanes is also secreted from the under-surface of ladybird tarsi aiding adhesion onto smooth surfaces (Kosaki & Yamaoka, 1996). Hemptinne *et al*. (2000c) speculate that these similar molecules, with different context dependent messages, are an example of semiochemical parsimony. The alkane semiochemicals of larval tracks show some degree of persistence. Ten-day-old fourth-instar larval tracks of *A. bipunctata* are sufficient to prevent oviposition in gravid females (Hemptinne *et al*., 2001). Other coccinellids studied include *C. septempunctata*, *C. limbifer* and *S. undecimnotata* (Růžička, 2002). It appears persistence of oviposition-deterring semiochemical tracks varies between species.

Coccinellids refrain from ovipositing at sites where there are few aphids present (Dixon, 1959). It has been established that aphidophagous ladybirds lay most of their eggs over a relatively short period of time early in the development of aphid colonies (Hemptinne *et al*., 2000a), the 'egg window' (Dixon, 1997). The window opens when aphids are abundant enough for sufficient survival of larvae developing from eggs. 'Closing of the window' probably occurs when conspecific larvae become so abundant in a patch that any further eggs laid are likely to be cannibalized (Hemptinne *et al*., 1992). Increased oviposition with prey density may simply result from the correlation between satiation level and oviposition rate (Banks, 1954). External aphid-associated cues, however, may also stimulate increased oviposition: oviposition by coccinellids can be triggered by chemical traces of their prey (Evans & Dixon, 1986).

The current study considers the nature and persistence of the effects of con- and heterospecific tracks on oviposition in the previously unstudied larch ladybird, *Aphidecta obliterata*. Any results will contribute usefully to an expanding framework of knowledge allowing us to further understand the extent of oviposition-deterring behaviour in response to larval tracks. The effects of varying aphid density while simultaneously varying the conspecific larval track contamination of filter paper substrates is also examined, allowing us to undertake a multivariate analysis and consider the combined effects of both variables (aphid density and oviposition-deterring semiochemical concentration) on oviposition behaviour in *A. obliterata*. The study then determines whether increased oviposition rate with aphid density can be partly attributed to chemical cues from aphids stimulating oviposition, rather than solely satiation-induced effects. Finally we test Hemptinne *et al*.'s (2000c) hypothesis of semiochemical parsimony by considering whether *A. obliterata* egg surface chemicals also inhibit oviposition.

Materials and methods

Insect culture

Larch ladybirds *Aphidecta obliterata* and two-spot ladybirds *Adalia bipunctata* were reared at $20°C \pm 2°C$ and a photoperiod of 16 h light and 8 h darkness, kept in 5-l plastic containers, which also included a piece of corrugated filter paper on which the ladybirds often laid eggs. Each day, the box was cleaned of debris and a fresh filter paper placed inside. Any filter papers containing eggs were transferred to an 18 cm Petri dish and incubated under the same laboratory conditions as the adults. Larvae hatching from eggs were kept in the same conditions. Each day, adults and larvae were fed an excess of aphids. *Aphidecta obliterata* were preferentially fed on an excess of bird-cherry–oat aphids, *Rhopalosiphum padi* (Linnaeus) from the laboratory culture (described below). If the cultures became exhausted, spruce aphids *E. abietinum*, rose aphids *Macrosiphum rosae* (Walker) and artificial food mix (Majerus & Kearns, 1989) were used to supplement the diet. *Adalia bipunctata* were preferentially reared on an excess of pea aphids *Acyrthosiphon pisum* (Harris). If these were unavailable then spruce aphids *E. abietinum*, rose aphids *M. rosae*, nettle aphids *Microlophium carnosum* (Theobald) and artificial food supplement was used. Once a week the adults were transferred to clean containers to stimulate egg laying. Lacewing larvae, *Chrysoperla carnea* (Stephens) (Neuroptera: Chrysopidae) were obtained as third instars (supplier: the 'Green Gardener®') and fed a similar diet to *A. bipunctata*.

Female ladybirds were used in the experiments. Ladybirds were sexed under a low power dissecting microscope (Majerus & Kearns, 1989). After sexing, females were kept in 5-l plastic boxes with approximately 25 individuals per box.

Broad bean plants (*Vicia fabae*), obtained from Nickerson-Zwaan®, were kept in the laboratory to culture pea aphids *A. pisum* and barley plants (*Hordeum vulgare* L.) (same supplier) used to culture bird-cherry–oat aphids, *R. padi*. If the cultures became exhausted, spruce *E. abietinum*, rose *M. rosae* and nettle *M. carnosum* aphids were collected from outside the laboratory.

Searching behaviour

To establish the effect of larval secretions on the searching behaviour of adult larch ladybirds, a choice test was carried out. Four third-instar *A. obliterata* larvae were kept in a 4.5 cm diameter Petri dish containing a 4.25 cm filter paper in the base. After 4 h the larvae were returned to the stocks and the filter papers were removed. The choice test arena involved a 4.5 cm Petri dish with half a clean filter paper and half a paper that had previously been stored with the larvae. An adult female *A. obliterata* was then placed in the Petri dish, covered with a non-airtight lid, and left for 5 min. After this initial time the location of the ladybird was noted down every minute for 30 min. This procedure was repeated 20 times.

Oviposition deterrence by con- and heterospecific tracks

Aphidecta obliterata females were offered a choice of oviposition sites (contaminated with larval tracks or uncontaminated). A 4.25 cm filter paper was placed inside each of four 4.5 cm Petri dishes. Two, five or ten fourth instar larvae of *A. obliterata* were placed inside each dish. One dish contained no larvae as a control. Larvae were allowed to remain in the dishes for 3.5 h to enable larval pheromones to adequately contaminate the filter paper, without being so long that cannibalism occurred. Larvae were then removed and faecal spots brushed off each filter paper using a fine paintbrush. Each filter paper was labelled with a number using a ballpoint pen, referring to the number of larvae contained in each dish. The filter paper in the dish which had held no larvae was also labelled with a 'zero'. It is assumed that an approximately equal amount of ink was marked on each paper, therefore this should not affect the results. Each filter paper was folded in a similar way to make it corrugated and a small piece of Blu-tack® attached to the centre of one side. The four filter papers were then secured onto the base of an 18 cm Petri dish in a square arrangement so that each filter paper was equidistant from the others and the centre of the square arrangement in the centre of the Petri dish (i.e. so that differences in oviposition rate on the different filter paper substrates could not be attributed to effects of spatial positioning; light on the Petri dishes was from directly above and the external environment in the laboratory was relatively uniform). Ten satiated *A. obliterata* females were then placed into the large Petri dish and left for 24 h. A preliminary investigation found that sometimes eggs observed part way through the 24 h period were not always present at the end of experiment. Therefore the number of eggs present on each filter paper was recorded at intervals of 5 and 10 h in addition to the final 24 h count, and any eggs thus known to have been cannibalized in the intervening periods were added to the final count. All replicates were started at approximately 0900 h each day. Infrequently, eggs were on the base of the Petri dish directly below a filter paper; these were assumed to have been dislodged during the experiment and included in the egg count of the paper which they were below. If eggs were present on the Petri dish, but not below any filter paper, they were omitted from the filter paper egg counts. Each test was replicated ten times.

The same procedure was followed using fourth instar *A. bipunctata* and third instar *C. carnea* to test for effects of heterospecific tracks.

Persistence

The persistence of the tracks produced by the larvae was investigated by first obtaining filter papers with *A. obliterata* larval tracks on using the method described above. These were then stored in ventilated plastic boxes for three, five, seven, nine or 11 days. On each of the appropriate days an adult female was placed in a Petri dish containing the contaminated paper along with an excess of *R. padi* aphids. As before, the number of eggs produced was recorded, and the procedure was repeated 20 times for each of the treatments.

Conspecific tracks and aphid density

An identical procedure to the one above for the investigation of effects of conspecific tracks on oviposition rate was employed, except that aphids were present during the 24 h oviposition period, allowing us to consider the effects of conspecific tracks and aphid density simultaneously. No, 200, 400 or 600 aphids were placed with the ten *A. obliterata* females for the duration of the 24 h period. To ensure the aphids did not escape during the experiment the sides of the Petri dish were coated in Fluon®. Eggs on each filter paper were then counted and recorded in the same way as before. A preliminary control investigation ensured that aphids in the Petri dish without predators, over a 24 h period, did not have a tendency to aggregate to any one of the filter papers in particular, showing that any differences in oviposition rate on the differentially contaminated filter papers were not due to differences in local aphid density. To control for variation in fecundity over time, each test (0, 200, 400 and 600 aphids) was carried out once per day. This ensured that any variation in fecundity over time (ladybirds have been shown to have triangular reproductive functions (Dixon, 2000)) was not mistakenly attributed to be due to changes in our explanatory variables. Each test was replicated ten times except for the 600 aphid treatment which was only repeated five times due to lack of available aphids.

Satiation

Before the experiment, ten *A. obliterata* females were starved for 12 h; all kept in an 18 cm Petri dish with a piece of 9 cm corrugated filter paper. Another ten females were kept in similar conditions except that excess aphids were present in the dish so that these females would begin the experiment in a satiated condition. For the experiment, each female was placed into an individual 9 cm Petri dish with a piece of corrugated 4.25 cm filter paper. The total number of eggs each female had laid after 12 h was recorded. Ten replications were carried out.

Prey-associated chemical cues

Before the experiment, ten pieces of 4.25 cm filter paper had 50 *R. padi* aphids pressed onto them. Another ten were left untouched as a control. Ten satiated *A. obliterata* females were each placed in an individual 18 cm Petri dish containing two pieces of 4.25 cm corrugated filter paper (one clean, one contaminated), arranged to mitigate spatial positioning biases. After 24 h, the relative number of eggs on each filter paper across the ten replications was recorded.
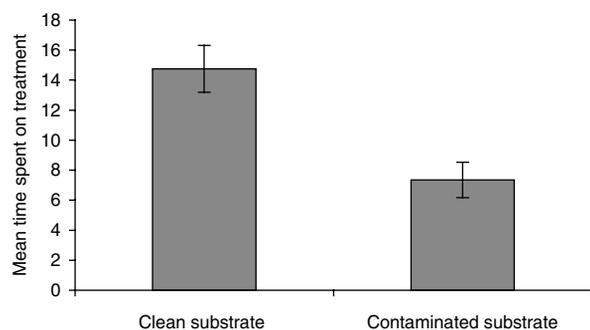
Fig. 1. Average time spent by 20 female *Aphidecta obliterata* on clean filter papers (14.75 ± 1.56 (S.E., $n = 20$) min) and filter papers contaminated with larval tracks (7.35 ± 1.18 (S.E., $n = 20$) min).

Egg surface chemicals

To determine whether egg surface chemicals had an effect on the oviposition rate of *A. obliterata*, 50 eggs were placed in a small vial and washed with 0.5 ml hexane solution (97%) (Hemptinne *et al.* (2000b) successfully used n-hexane to wash defensive chemicals off egg surfaces in order to quantify their effects on intraguild predation). Eggs used were approximately 3 days old, as eggs recently laid were too soft and presented a risk of contaminating the solution with egg yolk chemicals. Another vial contained 0.5 ml hexane, but no eggs. The vials were left for 1 h then, using a fine paintbrush, tracks were painted onto pieces of 4.25 cm filter paper. An 18 cm Petri dish was set up with two pieces of filter paper (one with hexane egg-wash tracks, the other with hexane control tracks) and ten satiated *A. obliterata* were placed inside and left for 24 h. The experiment was replicated ten times.

Statistical analysis

The experiments concerning oviposition deterrence by con- and heterospecific tracks and persistence of oviposition-deterring semiochemicals were analysed using ANOVA in the program 'R'. A generalized linear model was used for egg count data, as the response variable was not normally distributed (there were many cases when zero eggs were recorded). In some cases the scale parameter was greater than one (residual deviance/d.f. > 1), indicating the data were overdispersed, therefore the 'quasi' function was used to define a different family of error structures. Treatment degrees of freedom followed by error degrees of freedom are quoted in subscript beside each F value. Other data were analysed using t-tests; paired tests when appropriate. If the variances were significantly different, as deduced from a Fisher's F test, then variances were estimated separately for both groups, and a t-test with the Welch modification to the degrees of freedom was used. For the searching behaviour data, the time spent on uncontaminated filter papers compared with the time spent on larval-track contaminated filter paper was non-independent. Therefore the proportion of time spent on uncontaminated papers was calculated and a Wilcoxon's signed rank test was used to determine whether the mean was significantly greater than 0.5.
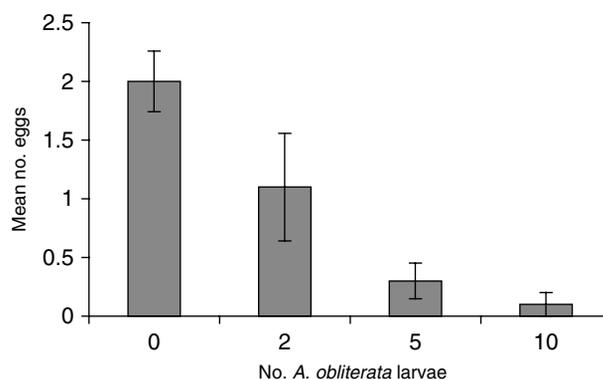

Fig. 2. Mean number of eggs laid by *Aphidecta obliterata* females over 24 h on four filter paper substrates contaminated with tracks of different numbers of conspecific larvae. Bars indicate standard errors of means.

Results

Searching behaviour

Aphidecta obliterata females spent significantly more time on clean filter papers compared with filter paper contaminated with conspecific larval tracks (Wilcoxon's signed rank test: $P < 0.01$, $n = 20$) (fig. 1). The average percentage of times which the females were found on each of the substrates was 33% (147/442 occasions) for the contaminated filter paper and 67% (295/442 occasions) on the clean filter paper.

Oviposition deterrence by con- and heterospecific tracks

Conspecific larval tracks significantly inhibited oviposition by *A. obliterata* females (ANOVA: $F_{1,38} = 10.665$, $P < 0.01$). In addition, the oviposition-deterring effects of conspecific larvae were positively density dependent, with increasing larval density increasing the degree of oviposition inhibition (fig. 2). The control treatment (zero larvae) was significantly different compared with all the larvae treatments (ANOVA: $t = 4.011$, $P < 0.001$). The two-larvae treatment was significantly different to the five- and ten-larvae treatments ($t = 2.838$, $P < 0.01$). The five-larvae treatment, however, was not significantly different from the ten-larvae treatment ($t = 0.951$, $P = 0.34$, NS).

In contrast, using ANOVA with a four-level factor, contamination of filter paper substrates by *A. bipunctata* larvae had no significant effect on oviposition rate of *A. obliterata* females (ANOVA: $F_{3,36} = 1.510$, $P = 0.23$, NS) (fig. 3). Model simplification, however, led to a marginally significant single-degree-of-freedom contrast between the uncontaminated control (zero larvae) and the larval treatments (ANOVA: $t = 2.126$, $P < 0.05$). The different larval treatments (two, five and ten larvae) were not significantly different (ANOVA: $t = 4.82e^{-14}$, NS).

Similarly, larval tracks of the chrysopid *C. carnea* did not significantly affect oviposition by *A. obliterata* females (ANOVA: $F_{3,36} = 2.739$, $P = 0.058$, NS) (fig. 4). There was a significant difference between number of eggs laid in the highest density of *C. carnea* treatment compared with the control (ANOVA: $t = 2.211$, $P < 0.05$). This ten-larvae treatment, however, was not significantly different to the other treatments combined (ANOVA: $t = 1.893$, $P = 0.066$, NS).
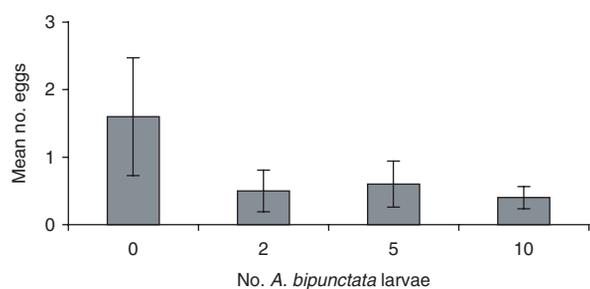
Fig. 3. Mean number of eggs laid by *Aphidecta obliterata* females over 24h on four filter paper substrates contaminated with tracks of different numbers of *Adalia bipunctata* larvae. Bars indicate standard errors of means.
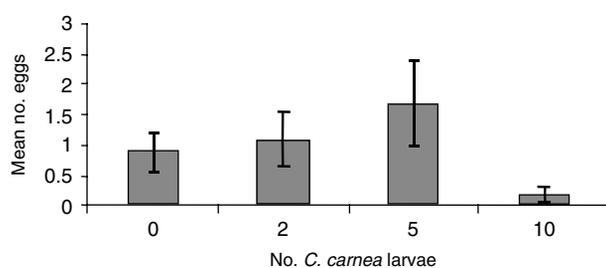

Fig. 4. Mean number of eggs laid by *Aphidecta obliterata* females over 24h on four filter paper substrates contaminated with tracks of different numbers of *Chrysoperla carnea* larvae. Bars indicate standard errors of means.

Persistence

Age of larval track was found to have a significant effect on the number of eggs laid by *A. obliterata* females (ANOVA, $F_{2,137} = 4.6273$, $P < 0.05$). To obtain the minimum adequate model the age of tracks was collapsed into three levels: control, fresh tracks (1–3 days) and old tracks (5–11 days). Fresh tracks elicited a significantly different oviposition rate than the uncontaminated control (ANOVA: $t = 2.791$, $P < 0.01$). Oviposition response to old tracks, however, was not found to be significantly different to the control (ANOVA: $t = 1.150$, $P = 0.252$, NS) (table 1).

After the initial deterrent effect from the production of larval tracks, the total number of eggs produced increased on each of the following days. The numbers of eggs produced on subsequent days formed a linear relationship with the age of the tracks, with a high correlation coefficient ($r^2 = 0.96$) (fig. 5).

Conspecific tracks and aphid density

A factorial two-way ANOVA was used to analyse the results. Both explanatory variables (larval tracks and prey density) had a significant effect on oviposition rate of *A. obliterata*: Increasing the degree of conspecific larval track contamination of filter papers significantly inhibited oviposition by *A. obliterata* females (ANOVA: $F_{3,136} = 18.149$, $P < 0.001$). Simultaneously, increasing the density of aphid prey present significantly increased oviposition rate (ANOVA: $F_{3,136} = 25.256$, $P < 0.001$) (fig. 6). There was no significant difference, however, between the 400 and 600
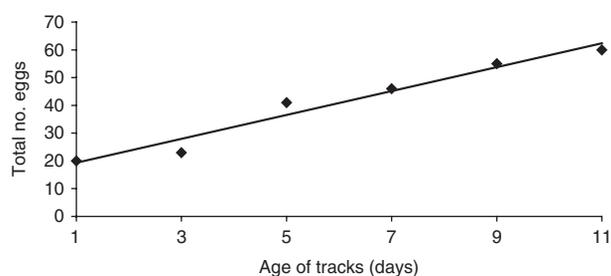

Fig. 5. Linear relationship between age and increase in number of eggs produced. The line representing the relationship has the equation $y = 4.3x + 15.03$ ($r^2 = 0.96$).
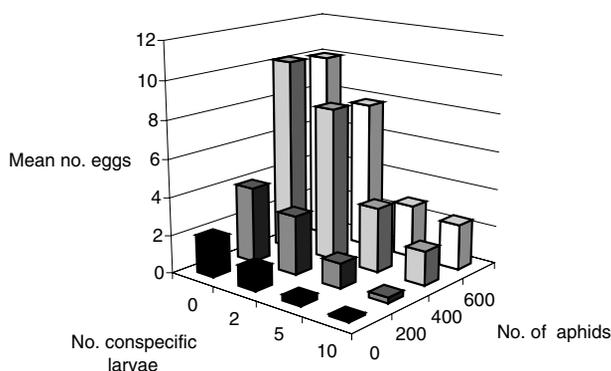

Fig. 6. Mean number of eggs laid by *Aphidecta obliterata* females over 24h on filter paper substrates differentially contaminated with conspecific larval tracks across a range of prey densities. Standard error bars have been omitted for clarity of expression.

aphid treatments and these could be combined with no significant loss in explanatory power to the minimum adequate model (ANOVA: $F_{1,136} = 0.0127$, $P = 0.91$, NS). Therefore at very high aphid densities (>400) there was no significant further increase in oviposition (fig. 7). This suggests there is some upper threshold of aphid density at which maximum oviposition occurs. Beyond this threshold, further increases in aphid density have little effect on oviposition rate of *A. obliterata*.

There was no significant interaction between prey density and contamination by larval tracks (ANOVA: $F_{9,124} = 0.4564$, $P = 0.9$, NS).

Satiation

Aphidecta obliterata females starved 12h prior to the experiment laid significantly fewer eggs than those satiated when the experiment began ($t = 3.76$, df $= 18$, $P < 0.001$), with an average oviposition rate of 4.0 ± 2.2 (S.E., $n = 10$) per female per 12h, compared with 7.9 ± 2.4 (S.E., $n = 10$) for satiated individuals.

Prey-associated chemical cues

Oviposition rate of *A. obliterata* females did not differ significantly between filter papers contaminated with aphid chemicals and clean filter papers (control) ($t = 0.2095$, d.f. $= 9$,
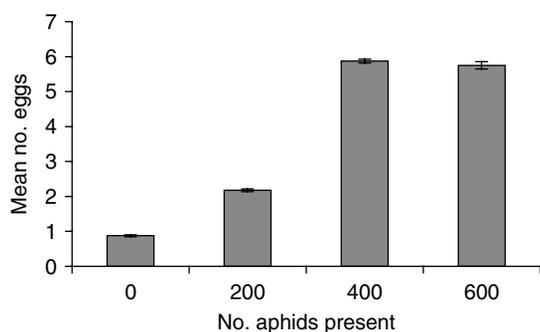
Fig. 7. Mean number of eggs laid by *Aphidecta obliterata* females over 24 h, averaged over all four larval treatments, to show the effect of increasing aphid density on oviposition rate. Bars indicate standard errors of the means. Same letters above bars indicate no significant difference between the treatments (ANOVA, $P < 0.05$).

$P = 0.84$, NS). The average number of eggs laid per 10 females on clean papers was 3.8 ± 1.2 (S.E., $n = 10$) compared with 4.3 ± 1.9 (S.E., $n = 10$) on papers contaminated with pressed aphids.

Egg surface chemicals

Contaminating the filter papers with the chemical extract of the surface chemicals from conspecific eggs reduced oviposition from an average of 6.0 ± 1.5 (S.E., $n = 10$) eggs per 10 females on clean papers, to 2.6 ± 0.5 (S.E., $n = 10$) eggs per 10 females on contaminated papers. The difference between the means was close to significance, but above the conventional Type I error margin ($\alpha = 0.05$) ($t = 2.134$, d.f. $= 11$, $P = 0.0559$).

Discussion

Oviposition deterrence by con- and heterospecific tracks

Aphidecta obliterata is significantly less likely to oviposit on sites contaminated with pheromones from conspecific larval tracks and the deterrence effects of these pheromones appear to be positively dependent on the density of larvae present, thus adults can determine the relative densities of larval tracks. Similar effects of conspecific larval tracks in other coccinellid species include *A. bipunctata* (Doumbia *et al.*, 1998), *C. septempunctata* (Růžička, 1997; Doumbia *et al.*, 1998), *C. limbifer* and *S. unidecimnotata* (Růžička, 2001). Originally it was assumed that oviposition deterrence occurred in relation to the frequency of encounters with larvae (Hemptinne *et al.*, 1992). It is clear, however, that an alternative mechanism that does not rely on physical encounters, exists to assess the density of conspecific larvae: oviposition-inhibition by oviposition-deterring semiochemicals. The frequency of female contact with a network of oviposition-deterring tracks is likely to be higher than the frequency of female encounter with the larvae (Růžička, 2001). Oviposition-deterrence in response to larval pheromones has evolved as a patch quality-assessment and response adaptation to reduce the risk of intraguild predation and increase the availability of prey for developing offspring. It reduces the risk of cannibalism and competition and allows coccinellids to synchronize generations with

Table 1. Number of eggs laid by *Aphidecta obliterata* females on filter papers contaminated by conspecific larval tracks of different ages. Displayed are means, sample size (n) and standard errors (S.E.).

Age of tracks (days)	n	Mean eggs laid (and S.E.)
Fresh (1–3 days)	40	1.08 ± 0.42
Old (5–11 days)	80	2.53 ± 0.37
None (control)	20	3.60 ± 0.91

transient aphid colonies. Density of larval tracks positively correlates to degree of egg cannibalism both under laboratory conditions (Dixon, 2000), and in the field (Mills, 1982). Cannibalism can be a major source of egg and early instar larval mortality in aphidophagous coccinellids (Agarwala & Dixon, 1992; Agarwala *et al.*, 1998; Gagné *et al.*, 2002). High densities of competing larvae result in smaller individuals with reduced fecundity in adulthood (Dixon, 2000). This is especially true in the competitive environment of patchy resources (Agarwala *et al.*, 2003). Also, exceeding the optimum number of predators per patch may severely restrict the rate of increase of aphid prey and cause an earlier collapse of the colony (Hemptinne & Dixon, 1997). On average, aphid colonies rarely last for more than a month (Hemptinne & Dixon, 1997). The total development time of *A. obliterata* larvae depends on the temperature, but ranges from 38 to 41 days (Wylie, 1958). If eggs are laid too late in the development of an aphid colony, the larvae will not mature before prey becomes scarce. The closing of the 'egg window' (the relatively short period of time, in comparison with aphid colony development, over which aphidophagous ladybirds lay most of their eggs), is likely to be induced by the presence of conspecific larval tracks. This form of habitat assessment is probably a common feature of insects that exploit resources that vary in abundance over time (Hemptinne *et al.*, 1992). Thus it appears that coccinellids may not be required to judge the age of an aphid colony through aphid associated cues, if they instead use oviposition cues from conspecific larvae. One drawback of this mechanism is that previously unexploited aphid colonies at any stage of development, if they had no resident predators, would induce gravid females to lay eggs, even if these colonies are past the optimum temporal window for egg-laying. The relative importance of cannibalism, competition and aphid colony transience has not been considered and further work could proceed in this area.

The present study shows the searching behaviour of *A. obliterata* is affected by conspecific larval tracks. *Aphidecta obliterata* actively avoids areas contaminated with conspecific larval tracks. This behaviour alone would result in the reproductive response described above. Alternatively, coccinellids may actively withhold oviposition in response to the oviposition-deterring semiochemicals. The exact mechanism of oviposition inhibition in response to these semiochemicals has yet to be elucidated.

In regards to the persistence of *A. obliterata* oviposition-deterring semiochemicals, larval tracks were found to significantly deter oviposition by conspecific females for up to three days. There was a strong linear relationship between the age of tracks and the number of eggs laid, thus implying a constant rate at which the oviposition-deterring semiochemicals decay or evaporate ($r^2 = 0.96$). The strong

persistence of these semiochemicals is likely to relate to their chemical composition. Larval tracks of *A. bipunctata* consist largely of alkanes, mostly methyl branched and straight chain hydrocarbons, whose stability results from their saturated nature preventing oxidation (Hemptinne *et al.*, 2001). The persistence time of larval oviposition-deterring semiochemicals is an emergent property of the chemicals that comprise them, but it is also likely to have fitness effects on gravid females. It is therefore tempting to speculate that persistence times will be shaped by evolution to the benefit of the egg-laying female. This is however, invalid; only fitness effects on the larvae emitting the tracks present selection pressures on the persistence time of oviposition-deterring semiochemicals. Low persistence oviposition-deterring semiochemicals will be selected against as larvae face increased competition from new predators on their patch. High persistence oviposition-deterring semiochemicals benefit the larvae, but only up to a point as there is a limited time until larvae pupate, emerge as adults and leave the patch. There may also simply be a maximum threshold to the stability of the chemicals that comprise oviposition-deterring semiochemicals. Previous studies with larval tracks of other species report a range of oviposition-deterring semiochemical persistence from only one day (Růžička, 2002), to ten days or more (Dixon, 2000; Hemptinne *et al.*, 2001).

The present study confirms that, like other coccinellid predators, the larvae of *A. obliterata* also produce oviposition-deterring tracks. In concurrence with previous studies of *A. bipunctata* by Doumbia *et al.* (1998) and Hemptinne *et al.* (2001), and *H. axyridis* by Yasuda *et al.* (2000), the adults were deterred from ovipositing by the presence of conspecific tracks, but were generally unaffected by those of hetero-specifics. In the present study, tracks of *A. bipunctata* and *C. carnea* larvae induced no significant overall response by *A. obliterata* females. There were, however, some marginally significant effects of contrasts between treatments. This offers some evidence for oviposition effects of heterospecific tracks, although the marginal significance and small sample size dictate the necessity for further empirical tests. Although heterospecific tracks are usually found to be ineffective deterrents, the finding is not unprecedented. Růžička (2001) found that heterospecific tracks of *C. septempunctata* and *S. undecimnotata* did deter oviposition between these two coccinellids. These two species are sympatric (Růžička, 2001). A later study also revealed that coccinellids can be deterred from ovipositing by the presence of chrysopid tracks (Růžička, 2003). It is possible that coexisting species which share a common, limited resource and/or engage in heterospecific predation of eggs and larvae may impose adequate selection pressures for the evolution of heterospecific semiochemical detection and response mechanisms. Persistence of semiochemicals is, of course, mediated by fitness effects on the emitter but in this case deterring competing heterospecifics is of clear benefit to the emitter. Thus, in effect, the semiochemical would be a synomone facilitating interspecific communication between individuals to their mutual benefit. Considering the present study: *A. obliterata* and *A. bipunctata* are geographically sympatric (both widespread throughout Britain) yet they forage in different habitats. The habitat of *A. obliterata* comprises needled conifers of all ages, including isolated trees, natural and plantation woodlands. In contrast, *A. bipunctata* tend to forage on a diverse range of herbaceous

plants, shrubs and trees (Majerus, 1994). In addition, they also have different prey preferences: *A. obliterata* prefers to feed on adelgids, e.g. *Adelges picea*, *Adelges nüsslini* (Börner), although it will feed on some aphids, e.g. *E. abietinum* (Wylie, 1958). In contrast, *A. bipunctata* feeds on a diverse range of aphids (Majerus & Kearns, 1989). With regards to further study, *Scymnus suturalis* (Thunberg) and *A. obliterata* have been found admixed to aggregations of *Myrrha octodecimguttata* (Linnaeus) (all Coleoptera: Coccinellidae) on pine trees (Pulliainen, 1966). Perhaps *A. obliterata* is more likely to show heterospecific oviposition responses to *S. suturalis*?

Aphid density

Increasing density of aphid prey leads to significant increases in the oviposition rate of *A. obliterata* females. Thus a trade-off occurs between the amount of prey present (inducing oviposition) and the concentration of larval tracks (inhibiting oviposition) (fig. 6). Růžička & Havelka (1998) stated that tracks of larvae prevent egg-laying on plants in spite of aphid prey. This study considered both larval track density and prey density simultaneously and showed that patch assessment is mediated through at least two cues (prey density and oviposition-deterring semiochemical concentration) that trade off, and the relative intensity of these stimuli determines the readiness of *A. obliterata* to lay eggs.

Dixon (1959) reports a lower critical density of aphids for egg-laying and that this is determined by the minimum density of aphids required for the survival of first instar larvae. This study found no such lower limit. Even when no aphids were present some eggs were still laid. At low to high prey densities (0–400 aphids), the degree of oviposition-stimulation was positively correlated with the density of aphid prey present. At very high prey densities, there was no further positive correlation between oviposition and prey density, suggesting that there is some upper threshold of prey density at which maximum oviposition occurs. It was demonstrated that *A. obliterata* females show a maximum per capita egg production in relation to prey density of approximately 40 aphids per day. This supports findings by Agarwala & Yasuda (2001) showing the numerical response of the aphidophagous coccinellid *Menochilus sexmaculatus* (Fabricius) to increasing aphid density to be positive and sigmoidal in nature, similarly achieving a plateau at approximately 40 aphids per day.

Agarwala & Yasuda (2001) noticed that the ratio of eggs produced to dry mass of aphids consumed by *M. sexmaculatus* (conversion ratio), is highest at lowest prey densites (0–10 aphids per day). They take this finding to be in agreement with the preference of ladybird predators for laying eggs when aphid colonies are still small or growing as suggested by Hemptinne *et al.* (1992). However, even if prey:egg conversion rate is highest at low prey densities, the numerical response is still clearly positive and larger aphid colonies will receive more eggs, contradicting the above view. It is more likely that conspecific larval pheromone cues are the main mechanism by which ladybirds respond to aphid colonies late in development (which will not support new eggs), with an inverse numerical response, i.e. closing the 'egg window'. Larval tracks have been shown to have a obvious inhibitory effect on oviposition, whereas Agarwala

CHEMICAL COMMUNICATION

STRUCTURAL FUNCTION

Egg surface chemicals
SIGNALLING TOXICITY

Larval tracks
OVIPOSITION
DETERRENCE

Elytra compounds
MATE RECOGNITION

SEMIOCHEMICAL
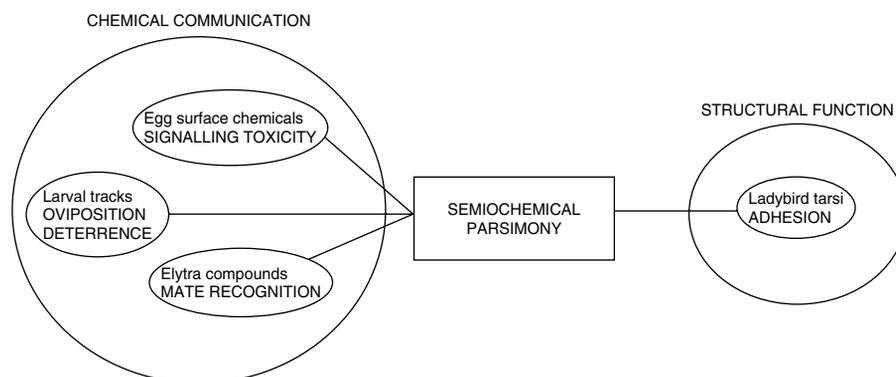PARSIMONY

Ladybird tarsi
ADHESION

Fig. 8. Diagram of the semiochemical parsimony occurring in ladybirds. Similar alkanes are claimed to be used on egg surfaces, elytra compounds and in larval tracks, as intra- and interspecific chemical messengers (Hemptinne *et al.*, 1998, 2000c). The same compounds have also been found to function in adhesion to smooth surfaces (Kosaki & Yamaoka, 1996).

& Yasuda's (2001) numerical response is still clearly positively correlated with prey density even if prey:egg conversion rate does show some small tendency to decline at higher prey densities.

Age structure of prey colony may also be an important factor affecting coccinellid offspring success. The density of smaller aphids must be high enough for neonates to obtain their first meal. First instar coccinellids are inefficient at capturing prey and their survival relies on the successful obtainment of their first meal soon after they leave the egg case (Dixon, 1959). Although co-existing with conspecifics can pose dangers from cannibalism, there are also advantages related to social feeding, where larvae share prey captured by other individuals (Hemptinne *et al.*, 2000b). Whether gravid coccinellid females use aphid colony age-structure in assessing patch quality is yet undetermined.

Satiation and prey-associated olfactory cues

Increasing the density of aphid prey present stimulates oviposition in *A. obliterata*, as described above. It has not been determined however, whether this increased oviposition is a behavioural response to externally detected aphid allelochemicals, or simply an increased fecundity facilitated by satiation, i.e. an internally mediated response. In this experiment it was shown that previously satiated females lay significantly more eggs than those starved for 12 h prior. Thus satiation is an important contributing factor to the increased oviposition response with increasing aphid prey densities. In contrast, olfactory cues from aphids did not significantly affect the oviposition rate of *A. obliterata*. These results are in accordance with the view that increased oviposition near aphid colonies results simply from the nutritional status of females, i.e. satiation facilitating increased oviposition (Banks, 1954). The results contrast with a study which claims that honeydew is an arrestant stimulus for searching coccinellids (Carter & Dixon, 1984), and also a study demonstrating that *C. septempunctata* withholds eggs in the absence of aphids, yet when aphid odours and honeydew are present (without aphids) oviposition occurs as normal (Evans & Dixon, 1986). Resolution of these conflicting studies may result from investigation into the effects of different

specific aphid-derived chemicals over a range of concentrations. It is possible that pressed aphids do not accurately represent the non-physical aspects of undisturbed aphid prey; alarm pheromones may be present at elevated levels affecting the oviposition response of females.

Egg-surface chemicals

Aphidecta obliterata females were not significantly deterred from oviposition by non-tactile cues from conspecific eggs in this experiment. The results, however, were on the margin of significance. The means of the two treatments (control and egg-surface chemicals) were very different (6.0 ± 1.5 (S.E., $n = 10$) eggs per 10 females and 2.6 ± 0.5 (S.E., $n = 10$) eggs per 10 females respectively) but because of the large difference in variance a paired t-test was invalid. Further work with larger sample sizes may reduce the variance and lead to significant results. Avoiding sites with high concentrations of egg surface chemicals could provide similar fitness benefits to females as avoiding sites with conspecific larval tracks, namely increased offspring survival probability due to reduced cannibalism and competition, and increased food availability. Studies on *A. bipunctata*, however, failed to produce such a response to conspecific eggs or pupae (Hemptinne *et al.*, 1992). In contrast, the current study found results very close to significance. If this non-significance is simply a result of limited replication, then the discrepancy between this experiment and that of Hemptinne *et al.* (1992) may arise from the fact that the present study used egg surface chemical extract at high concentrations (50 eggs), yet Hemptinne *et al.* (1992) used only a single batch of whole *A. bipunctata* eggs. Egg surface chemicals would be present at a much lower concentrations and therefore fail to elicit a reproductive response. Hemptinne *et al.*'s (1992) experimental set up is much more typical of situations in the field, where a female infrequently encounters batches of eggs together. Therefore the observed (marked, but not significant) response in the current study with *A. obliterata* may not be adaptive, but simply artefactual. An explanation for the response is that these chemicals found on egg surfaces have similar structures to the oviposition-deterring semiochemicals in larval tracks (as shown by the oviposition-deterring

response at high concentrations), but actually serve a different function. Blum (1996) was the first to suggest that some insects exploit their natural product with parsimonious versatility. Egg surface alkanes are important in signalling the toxicity of eggs to heterospecific predators (Hemptinne *et al.*, 2000c). Further work has shown these alkanes are also present on the surface of adult elytra and function in mate recognition (Hemptinne *et al.*, 1998). In addition, a similar mixture of alkanes is secreted from the under-surface of ladybird tarsi aiding adhesion onto smooth surfaces (Kosaki & Yamaoka, 1996). Thus it appears the same alkanes, also functioning in adhesion, are used to transmit several different context-dependent messages (fig. 8).

Implications for biocontrol

The ideal result of introducing a natural enemy as a biological control agent is to begin a persistent and stable interaction which will maintain pest numbers at equilibrium below an economic threshold. *Aphidecta oblite-rata* has been used in attempted biological control programmes in the past. Hodek (1973) reported that *A. obliterata* was imported from Germany to North Carolina to control *Adelges piceae*, the cause of considerable damage to *Abies* spp. The coccinellid was released in 1960 and 1963. Amman (1966) stated that after four years of survival it was reported as a permanent addition to the predator complex. There are, however, no quantitative reports of its efficiency as a biocontrol agent. In some cases, *A. obliterata* has been recommended as a potential biocontrol agent. Salom (1998), after preliminary studies demonstrated encouraging vorac-ity, recommended *A. obliterata* as a biocontrol agent for the hemlock woolly aphid. *Aphidecta obliterata* may also be an important natural enemy of the green spruce aphid, *E. abietinum*, a pest of spruce (*Picea*) spp., including Sitka spruce (*Picea sitchenisis*), Britain's main commercially grown tree (Carter & Halldorson, 1998).

There are a number or reasons why *A. obliterata*, and aphidophagous coccinellids in general, may make for poor biocontrol agents. Stabilizing the abundance of a pest well below an economic threshold is often achieved by a strong aggregative response (functional and numerical) to high densities of prey. The present study shows that the positive numerical response of *A. obliterata* to increasing prey density is weakened by its tendency to avoid ovipositing in patches already exploited by conspecific larvae. The numerical response of *A. obliterata* is important in determining spatial variation in predators (oviposition-deterring semiochemicals tend to cause predators to distribute themselves more evenly between patches). This spatial variation may have important implications for the stability of predator–prey interactions. Mathematical models often assume that predators choose prey patches independently of the distribution of other predators which leads to aggregation of risk of predation (Jansen *et al.*, 1997). With oviposition-deterring semio-chemicals at play, however, this is clearly not the case. Van Baalen & Sabelis (1993) relaxed this assumption and in a combination of the classic Nicholson-Bailey model and a game theoretical model they allow parasitiods and hosts to distribute themselves in an evolutionary stable manner. This resulted in a significant decrease in the parameter space in which the model achieved a stable equilibrium. Beddington *et al.* (1978) stated that differential exploitation of patches in a spatially heterogeneous environment provides the most likely mechanism to account for known biological control successes. This contradicts Růžička's (1998) statement claiming that oviposition-deterring semiochemicals, causing a more even distribution of predators between patches, may allow them to achieve a higher efficiency of aphid control.

Ladybirds also tend to become satiated at a relatively low prey density. Thus the maximum reproductive response occurs at low prey densities thereby contributing to the destabilization of the predator–prey interaction (Hemptinne *et al.*, 1992).

To summarize, the effects of ladybird oviposition-deterring semiochemicals on their numerical response tends to affect the spatial variation of these predators, causing them to be distributed more evenly across prey patches. This dampening of the aggregative response of predators to heterogeneous prey patches leads to destabilization of the predator–prey interaction. This instability is further accentuated by the low satiation threshold of predators, leading to a maximum reproductive response at low prey densities thereby further counteracting any aggregation of predation risk faced by patches of high prey density.

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