

Attack strategy of ladybird beetles (Coccinellidae): factors shaping their numerical response

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Summary. Temporal changes in aphid abundance pose a considerable challenge to ovipositing aphidophagous ladybirds, as in order to maximize their fitness they need to synchronize their reproduction with the early development of aphid populations. Field census data and laboratory experiments were used to determine how ovipositing females of the two-spot ladybird, *Adalia bipunctata* (L.), assess whether an aphid population is suitable for exploitation. In the field, two-spot ladybirds usually laid eggs well before aphid populations peaked in abundance. In the laboratory they showed a marked reduction in their reproductive numerical response in the presence of larvae of their own species but not of other aphidophagous ladybirds. At the highest aphid density this was not a consequence of competition for food between larvae and ovipositing females. In the presence of conspecific larvae gravid females were very active and as a consequence more likely to leave an area, and when confined with other conspecific females or larvae laid fewer eggs and later than females kept on their own. The extent of the inhibition of egg laying is negatively correlated with the rate of encounter with larvae. Thus it is proposed that gravid females appear mainly to use the presence of conspecific larvae to assess the potential of an aphid colony for supporting the development of their offspring.

Key words: Ladybird beetles – Oviposition – Numerical response

The ability of ladybirds to control aphid populations at levels below economic thresholds depends on their foraging and reproductive responses to patchily distributed prey (Begon et al. 1986; Kareiva and Odell 1987). Although their foraging behaviour has received a lot of attention (Banks 1957; Dixon 1959; Carter and Dixon

1982, 1984), their reproductive behaviour has been largely ignored. Recently much interest had been shown in insect reproductive strategies (e.g. Godfray 1987; Mangel 1987; Parker and Courtney 1984). However, models of the reproductive behaviour of predators generally assume that egg production is directly regulated by the rate of food consumption (Beddington et al. 1976; Gutierrez and Baumgaertner 1984), which is unlikely to be the most important factor governing the oviposition strategy of aphidophagous ladybirds as the survival of their offspring depends on the location and synchronization of oviposition with the early development of a relatively ephemeral food resource: aphid populations.

Most aphidophagous ladybird beetles have a developmental time of approximately one month in the field (Obrycki and Tauber 1981). Aphid colonies persist for relatively short periods of time and show rapid changes in abundance, often in response to changes in host-plant quality. Under these circumstances, ladybirds will only breed successfully if they are able to synchronize the growth of their larvae with the development of an aphid population. The survival of young larvae depends on the abundance of young aphids at the time of egg hatch (Dixon 1959), and the larvae must complete their development and pupate before prey become scarce due to aphid emigration or to depredation by coccinellids.

If the availability of food is the only factor involved in egg production and oviposition, as theory predicts, eggs are likely to be laid where aphids are shortly to become scarce. One way to avoid this is to assess the quality as well as the quantity of the resource. Evans and Dixon (1986) have shown that females on the verge of oviposition do respond to cues indicating the presence of aphids. In the absence of such cues, females can withhold eggs for several hours. Therefore it is likely that oviposition is in part triggered by certain qualitative features of aphid populations. In this paper, we use field census data to determine whether ladybirds show a preference and oviposit with young aphid colonies and laboratory experiments to determine how ladybirds assess whether an aphid colony is suitable for exploitation.

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Materials and methods

Experiments were conducted in the laboratory on females of *Adalia bipunctata* (L.) fed pea aphids, *Acyrtosiphon pisum* (Harris). The stock culture of beetles was kept in an environmental chamber at 16° C and 16L:8D photoperiod. Groups of 40 ladybirds (sex ratio 1:1) were kept in containers (6 × 17.5 × 11.6 cm) with damp tissue and a piece of corrugated filter paper (10 × 15 cm). The beetles were between 1 and 2 months old. At that age, they will have been fertilized and are ready to lay eggs (Hemptinne 1989). All the experiments were performed in an environmental cabinet at 20° C and 16L:8D photoperiod.

Reproductive numerical response

Female ladybirds were taken from the stock culture and kept individually in a 9-cm diameter Petri dish (approximately 150 cm²) together with 1, 2, 5, 10 or 20 aphids. It was estimated that these densities were representative of field conditions (Mills 1982). Aphids of approximately the same size were selected (average weight: 3.7 ± 1.0 mg). Petri dishes and aphids were changed daily. The females were allowed 48 h to acclimatize and then their egg production was recorded over the following 24 h. Twenty replicates of each aphid density were used. In a second treatment the above conditions were each replicated 15 times and three fourth-instar *A. bipunctata* larvae were added to each Petri dish at the beginning of the third day. In both treatments, the number of aphids consumed was noted.

Oviposition behaviour

The field observations were based on an analysis of both published and unpublished census data. The objective of this was to determine whether ladybirds restrict oviposition to certain periods of the year and only oviposit close to aphids in populations that are at a particular stage of development.

At 0900 hours, females were transferred from the stock culture to 5-cm diameter Petri dishes and fed an excess of mixed instars of pea aphid (average total weight provided: 40 mg). There were 30 replicates of three treatments: females kept singly (i.e. control) and two or three females confined together. The egg production was recorded 3, 6 and 9 h after the experiment began.

In addition the number of eggs laid by females kept singly was compared with that of females kept with one batch of two-spot ladybird eggs, with three fourth-instar *A. bipunctata*, or *A. decempunctata* (L.) (ten-spot) or *Coccinella septempunctata* (L.) (seven-spot) larvae or with three *A. bipunctata* pupae. The Petri dishes were checked hourly for egg cannibalism, which is easily identified by the presence of a yellow stain where the eggs had been.

Interaction between ovipositing females and larvae

The activity of the ladybirds was observed between 0900 and 2100 hours. Individual beetles were kept with 20 aphids, with or without a fourth-instar larva, and on the third day the numbers of stationary ("inactive") and moving ("active") beetles were scored every 5 min over a period of 1 h 40 min (i.e. 20 times). There were 21 replicates of each treatment.

The effect of larval odour on oviposition was tested in a two-tiered chamber made of 5 cm diameter Petri dishes, with the floor of the upper chamber consisting of muslin. At 0900 hours, a female was introduced to the upper compartment and three fourth-instar larvae of the same species were placed in the lower compartment of each arena. Larvae were not used in the control. The adults were fed an excess of aphids and the eggs they produced were counted at 3, 6 and 9 h after the start of the experiment. The control was replicated 20 times and the treatment with larvae 19 times.

The responses shown by gravid females on encountering fourth-instar larvae were observed for 30 min during the interval 1000–1400 hours, which is the period of peak activity of ladybirds (Nakamuta 1987). An encounter, i.e. when a female touched a larva with her palps, was usually followed by one of three kinds of response: (a) "attack", when a female tried to bite the larva; (b) "avoidance", when a female immediately backed away; (c) "no response", when a female walked around or over the larva.

The effect on oviposition of the rate of encounter of gravid females with larvae was determined using females taken from the stock culture and placed singly in a Petri dish of 5, 9 or 15 cm diameter. They were allowed 15 min to acclimatize before fourth instar larvae were added. The encounter rates and responses of the females caged with different numbers of living or dead (killed by a short exposure to -18° C) larvae were noted. The numbers of larvae used were: in 15-cm Petri dishes: 1, 2 or 3 living or dead larvae; in 9- and 15-cm Petri dishes: 1 living larva. There were 30 replicates of each treatment. The non-normality of many of the results rendered it inappropriate to use a two-way analysis of variance and necessitated the use of nonparametric significance tests.

Results

Oviposition in the field

Theoretical predictions. Figure 1 shows the advantages of ladybirds synchronizing their reproduction with the early development of aphid populations. Generally the number of aphids on a plant increases dramatically and then declines rapidly with this cycle in aphid abundance lasting approximately 1 month. Ladybirds similarly take approximately a month to complete their larval development in the field (Obrycki and Tauber 1981). Thus the later in the cycle of aphid abundance ladybirds lay their eggs the less chance their larvae have of completing development. In addition the survival of hatching ladybird larvae depends on the abundance of small aphids. This is represented by the threshold density d_1 in Fig. 1 and is significantly higher than the density d_2 of aphids required for the survival of the final stage larvae (Dixon 1959). Thus if ladybirds are to complete their development they should restrict egg-laying to large aphid colo-

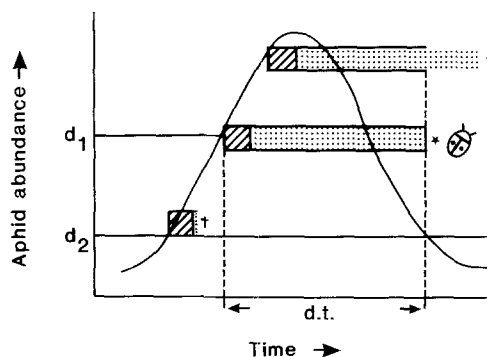


Fig. 1. The advantage of ladybird beetles synchronizing their reproductive effort with the early development of aphid populations. ▨ = egg laying, ▩ = larval development, (open means that larvae cannot complete their growth. (†) unsuccessful, (*) successful reproductive effort; d_1 and d_2 = threshold densities for the survival of first and fourth instar larvae, respectively; $d.t.$ = developmental time)

nies ($> d_1$) that are in the early stages of population development.

Field observations. A survey of the different habitats occupied by *A. bipunctata* revealed that the oviposition period of this beetle generally begins in the second week of May and lasts approximately four months (Hemptinne and Naisse, 1988). However, eggs were only observed in each habitat over a short period. For example, they only laid eggs on cereal plants during a 2-week period when the aphid population was increasing (Fig. 2), but eggs were found before and after this period on other species of plants. Moreover, an analysis of a large set of population census data for both cereal [*Metopolophium dirhodum* (Walk.), *Sitobion avenae* (F.)] and lime [*Eucallipterus tiliac* (L.)] aphids (A.F.G. Dixon, unpubl.; Hemptinne 1989; UEA Aphid Group, unpubl.) also revealed that generally eggs are laid well before aphid populations peak in abundance (Fig. 3; wheat fields: number of egg batches = 105, $\chi^2 = 94.54$, $P < 0.001$; lime trees: number of egg batches = 30, $\chi^2 = 39.22$, $P < 0.001$). This is in accordance with the theoretical predictions that females should have a very strong preference for ovi-

positing in aphid colonies that are at an early stage of development.

Reproductive numerical response

By 48 h the beetles fed 2 or more aphids per day had acclimatized to the experimental conditions and were producing a constant number of eggs per day (Table 1). The analysis of the reproduction over the next 24 h revealed that the minimum threshold for egg production was approximately one aphid per 150 cm². The average number of eggs laid increased up to 5 aphids/150 cm² and there was no significant difference between the average number of eggs laid at 5, 10 and 20 aphids/150 cm² (Fig. 3a). Measurements of aphid consumption suggest that aphid densities up to 5 aphids/150 cm² were not sufficient to meet the nutritional requirements of the females, which were only met at densities of 10 aphids/150 cm² and greater (Table 2). Food supply controls the reproductive response as the number of eggs laid is correlated with the number of aphids eaten ($r = 0.75$; $P < 0.001$).

The reproductive numerical response was very different in the presence of larvae. The minimum aphid density for egg production was 5 aphids/150 cm² (Fig. 4b) and although egg production increased with aphid abundance it was always lower than in the absence of larvae ($F = 10.022$; df 1, 4; $P < 0.05$; Fig. 4). There was also an increase in the number of aphids eaten and in the per-

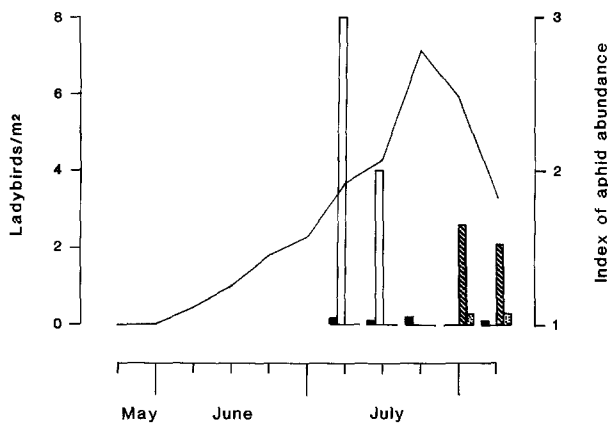


Fig. 2. Development of aphid (—) and ladybird (histogram) populations in a wheat field in 1985. Histogram: ■ = adult, □ = eggs, ▨ = larvae, ▩ = pupae. Aphid abundance as in Hemptinne and Naisse (1988) and coccinellids as in Hemptinne (1989)

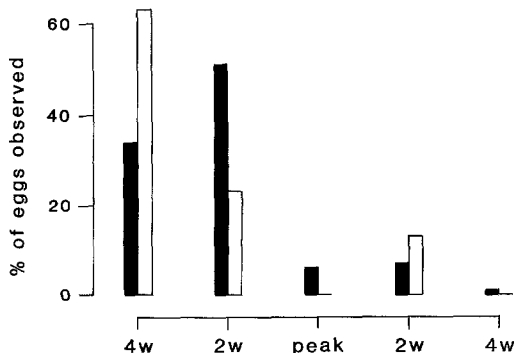


Fig. 3. Distribution in time, relative to peak aphid abundance, of ladybird egg batches in wheat fields (■) and on lime trees (□). Development of aphid populations expressed in weeks before and after the recorded peaks

Table 1. Number of eggs laid by females of *Adalia bipunctata* in successive 24-h periods at five aphid densities

Aphid density (No./150 cm ²)	Time (h)			F-ratio
	24 \bar{x} (SE)	48 \bar{x} (SE)	72 \bar{x} (SE)	
1	11.5 (2.1)	3.8 (1.1)	0.5 (0.3)	16.09***
2	14.0 (2.4)	7.1 (1.3)	7.0 (1.9)	4.34**
5	16.5 (3.0)	13.5 (2.2)	14.6 (2.4)	0.33NS
10	21.0 (2.0)	17.6 (2.3)	20.2 (2.4)	0.40NS
20	14.3 (3.2)	11.3 (1.7)	17.7 (2.8)	1.63NS
F-ratio	1.51 NS	8.90 NS	14.25***	

NS = not significant: $P > 0.05$; ** $P < 0.01$; *** $P < 0.001$

Table 2. The final daily average number of aphids eaten and the percentage of replicates in which all the aphids were eaten in the presence and absence of larvae at five prey densities

Aphid density (No./150 cm ²)	n	Larvae			
		Absent		Present	
		\bar{x} (SE)	%	\bar{x} (SE)	%
1	10	0.8 (0.1)	80	1.0 (0.0)	100
2	10	1.6 (0.2)	70	1.0 (0.0)	100
5	10	4.7 (0.1)	70	4.9 (0.3)	80
10	10	7.9 (0.5)	0	8.2 (3.1)	57
20	10	7.9 (3.2)	0	10.7 (5.3)	6

The experiment was run for 3 days

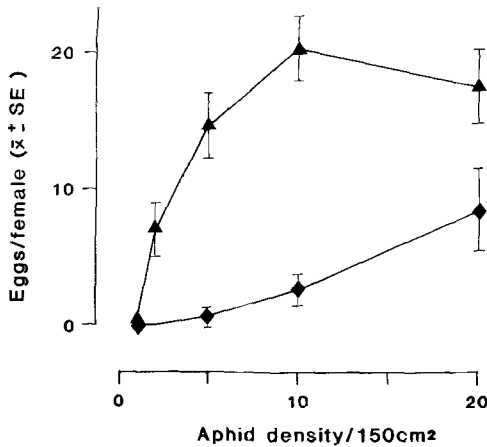


Fig. 4. Daily egg production of *Adalia bipunctata* at different aphid densities, in the absence (▲) and presence (◆) of fourth-instar larvae of their own species

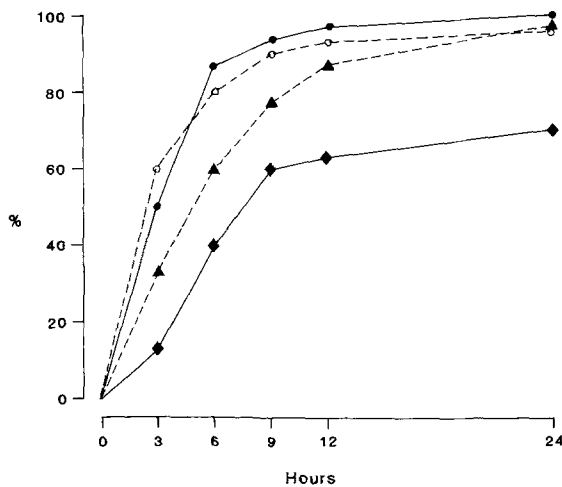


Fig. 5. The cumulative percentage of females of *Adalia bipunctata* laying their first batch of eggs after being placed in Petri dishes with aphids and subjected to one of the following treatments: (●)=1 female alone (control), (◆)=1 female and 3 fourth instar larvae, (▲)=1 female and 3 pupae, (○)=1 female and a batch of non-sibling eggs of their own species

centage of the cases in which all the aphids were consumed (Table 2). Competition for food between larvae and females probably had an impact on egg laying when 1, 2, 5 and 10 aphids were provided, as food supply was too low to meet the requirements of both larvae [10.2 mg/larva/day at 20° C (Mills 1979)] and females [30.0 mg/beetle/day at 20° C (J. Coffin, unpubl.)]. On the other hand, there was undoubtedly enough prey for females and larvae when 20 aphids were provided. Therefore at the highest aphid density it is unlikely that the low production of eggs was a consequence of food limitation.

Oviposition behaviour

Gravid females were reluctant to oviposit when other females were present, with significantly fewer eggs laid

Table 3. Average numbers of eggs laid by females of *Adalia bipunctata* during 3, 6 and 9 h in 5-cm Petri dishes in which they were kept singly or with 1 or 2 other females

Duration (h)	1 female \bar{x} (SE)	2 females \bar{x} (SE)	3 females \bar{x} (SE)
3	13.7 (2.2) ^a	3.6 (1.1) ^b	3.5 (0.7) ^b
6	16.2 (2.1) ^a	11.3 (1.2) ^a	6.7 (0.8) ^b
9	18.6 (2.1) ^a	14.2 (1.4) ^a	9.1 (0.9) ^b

In each line, means followed by different letters differ significantly ($P < 0.01$ for the means at 3 and 6 h; $P < 0.05$ for the means at 9 h)

after 3 h than in the control. After 6 h, females confined in pairs laid as many eggs as the control beetles. Those kept in groups of three laid markedly fewer eggs throughout the experiment (Table 3).

Similarly, the presence of conspecific larvae dramatically affected oviposition (Table 4). The average reduction with respect to the control was greatest after 3 h. This is not a consequence of egg cannibalism by larvae, which ate fewer eggs than the control females (proportion comparison: $u = 5.21$; $P < 0.001$). The differences in oviposition progressively decreased with the passage of time and no significant differences were apparent after 48 h. Females kept with larvae also laid their first batch of eggs later than control females (Fig. 5; Kruskal-Wallis test: $H = 27.72$, $P < 0.001$). However, the presence of eggs or pupae did not affect the number of eggs laid or time to first oviposition.

The presence of seven-spot or ten-spot ladybird larvae had a slight but statistically insignificant negative effect on oviposition (Table 5). However, as previously, the presence of two-spot larvae had a markedly negative impact on oviposition.

Interaction between gravid females and larvae

Beetle activity. There was no evidence that the level of activity changed with time and therefore the values recorded at 0900 and 2100 hours were pooled. The activity of females was significantly greater in the presence of larvae (Fig. 6; $\chi^2 = 65.76$, 1 *df*, $P < 0.001$). Females kept on their own in Petri dishes were scored as active as frequently as at rest (binomial test; $z = 0.54$, $P > 0.05$), whereas those confined with larvae were observed to move more frequently (binomial test; $z = 10.49$, $P < 0.001$). They also seemed to move more quickly than females kept on their own although this proved difficult to measure.

Mechanism. Larval odour had no significant effect on ladybird oviposition although the females exposed to the smell of larvae did lay slightly more eggs than the control beetles (Table 6).

The encounter rates varied significantly between treatments (Fig. 7; $F = 4.55$, $P < 0.001$). The average number of encounters with dead larvae was related to the number in the Petri dishes but this was not so for living larvae.

Females clearly responded differently when they en-

Table 4. Average numbers of eggs laid by females of *Adalia bipunctata* in 3, 6, 9, 24 or 48 h when kept singly or with their immature stages

Treatment	Duration (h)				
	3 \bar{x} (SE)	6 \bar{x} (SE)	9 \bar{x} (SE)	24 \bar{x} (SE)	48 \bar{x} (SE)
Control	11.8 (2.0) ^a	14.5 (1.8) ^a	16.5 (1.7) ^a	19.5 (1.6) ^a	31.4 (2.5) ^a
Eggs	9.1 (1.7) ^a	13.1 (1.4) ^a	14.7 (1.4) ^a	18.3 (1.8) ^a	32.0 (2.9) ^a
Larvae	2.3 (1.1) ^b	5.4 (1.5) ^b	9.8 (1.7) ^b	12.2 (2.0) ^b	23.6 (2.3) ^a
Pupae	6.8 (2.0) ^a	11.9 (2.3) ^a	14.8 (2.2) ^a	17.5 (1.9) ^a	29.1 (2.9) ^a

Treatment as described in text

In each column, means followed by different letters differ significantly ($P < 0.01$ for the means at 3 and 6 h; $P < 0.05$ for the means at 9 and 24 h)

Table 5. Average numbers of eggs laid in 3, 6 and 9 h by females of *Adalia bipunctata* kept in isolation or with larvae of their own and other coccinellid species

Duration (h)	Treatment			
	Control \bar{x} (SE)	2-spot larvae \bar{x} (SE)	7-spot larvae \bar{x} (SE)	10-spot larvae \bar{x} (SE)
3	7.6 (1.5) ^a	1.5 (1.1) ^b	3.7 (1.5) ^a	4.7 (1.4) ^a
6	10.3 (1.6) ^a	1.9 (1.1) ^b	5.6 (1.8) ^a	9.8 (1.9) ^a
9	11.8 (1.5) ^a	3.7 (1.4) ^b	8.7 (1.9) ^a	12.2 (2.0) ^a

Treatment as described in text

In each line, means followed by different letters differ significantly ($P < 0.01$)

Table 6. Average numbers of eggs laid by *Adalia bipunctata* when exposed to the odour of larvae of their own species

Duration (h)	n	Treatment			
		Control \bar{x} (SE)	n	Odour \bar{x} (SE)	t-test
3	20	9.5 (1.9)	19	10.9 (2.5)	0.4 NS
6	20	11.6 (2.2)	19	15.5 (2.6)	1.1 NS
9	20	13.6 (2.2)	19	17.8 (3.1)	1.1 NS

Treatment as described in text

NS = not significant, $P > 0.05$

countered dead and living larvae (Table 7; $\chi^2 = 387.08$, 2 *df*, $P < 0.001$). Of the encounters with dead larvae 63% failed to elicit a definite response whereas all encounters with living larvae resulted in avoidance or attack. Thus living larvae elicit a stronger response than dead larvae.

The production of eggs over 3 h was affected by the frequency of encounters between females and larvae during that period (Fig. 7; $F = 6.40$, $P < 0.001$). A progressive decrease in oviposition was observed when females were kept with increasing numbers of dead larvae with significant differences from the controls in the presence of 2 or 3 larvae (Dunnett test: control-1 dead larvae: $d = 5.37$, $P > 0.05$; control-2 dead larvae: $d = 8.13$, $P < 0.01$; control-3 dead larvae: $d = 9.37$, $P < 0.01$). The reduction in egg laying was significantly more pronounced in the presence of living larvae but not related to the number present: the average numbers of eggs laid did not differ between treatments (Newmann-Keuls test: $P > 0.05$) but were significantly lower than in the control

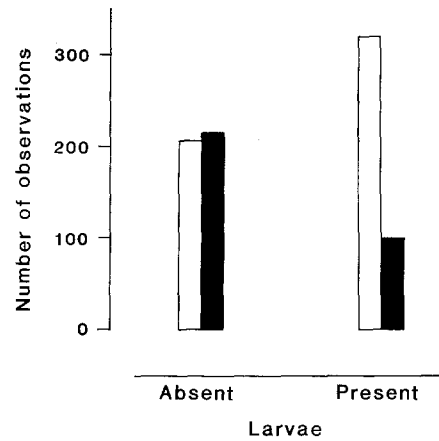


Fig. 6. Level of activity of female *Adalia bipunctata* kept singly or with a fourth instar larva of their own species. Level of activity: "active" (□) and "inactive" (■)

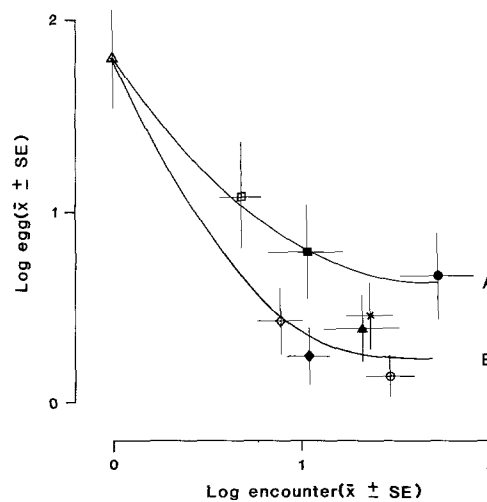


Fig. 7. The relation between the logarithm of the number of eggs laid in three hours by females confined in Petri dishes with different numbers of dead (A), or living (B) conspecific larvae and the logarithm of the number of encounters between these females and the larvae. One female in a 5-cm Petri dish: (Δ); female alone, (□) + 1 dead larva, (■) + 2 dead larvae, (●) + 3 dead larvae, (◆) + 1 living larva, (○) + 2 living larvae, (▲) + 3 living larvae; (X) a female + 1 living larva in a 9 cm Petri dish and (◇) a female + 1 living larva in a 15 cm Petri dish. Lines fitted by eye

Table 7. Nature of the responses shown by females of *Adalia bipunctata* on encountering living or dead fourth instar larvae of their own species (pooled data for females with 1, 2 or 3 larvae per Petri dish of 5-cm diameter)

	Larvae	
	Living	Dead
<i>n</i>	90	90
Encounters resulting in:		
attack	50	51
avoidance	338	114
no response	0	278
Total	388	443

n, number of replicates

(Dunnett's values > 7.37 ; $P < 0.01$). Females appeared to react to a cue associated with larvae, which acts over a short distance and is markedly stronger for living than dead larvae. For example, the average rate of encounter was similar for a female kept with 1 dead larva in a 5-cm diameter Petri dish or with 1 living larva in a 15-cm diameter dish ($\bar{x} = 0.29$ and 0.41 ; $t = 1.69$, 58 *df*, $P > 0.05$) but the females laid significantly fewer eggs when with living larvae ($\bar{x} = 8.3$ and 2.7 ; $t = 2.06$, 58 *df*, $P < 0.05$). Similarly, females confined with 2 living larvae produced fewer eggs than those kept with 2 dead larvae ($\bar{x} = 0.8$ and 5.6 ; $t = 2.40$, 58 *df*, $P < 0.05$) although the average rate of encounter with larvae was much the same in both treatments ($\bar{x} = 0.65$ and 0.45 ; $t = 1.96$, 58 *df*, $P > 0.05$).

Discussion

Temporal changes in aphid abundance (Dixon 1985) pose a considerable challenge to ovipositing aphidophagous ladybirds. They should synchronize their reproduction with the early development of aphid colonies because the survival of newborn ladybird larvae is very dependent on an abundance of young aphids (Dixon 1959). Oviposition late on in aphid population development could result in the older larvae being short of food and failing to complete their development. Thus, the optimum time for reproduction is a short period at the beginning of the development of an aphid colony, when the above two constraints are met (Hemptinne et al. 1990). Field surveys of populations of several species of aphids indicates that ladybird oviposition tends to be concentrated over a few days and to occur before the aphid populations reach peak abundance, whereas ladybirds can lay eggs continuously for at least 3 months (Hodek 1973). There are thus strong indications that ladybirds, as predicted, do prefer to oviposit close to aphid populations that are in an early stage of development.

Ladybirds respond to increase in prey abundance by increasing oviposition up to a maximum of 5 aphids/150 cm², above which *A. bipunctata* is satiated and the rate of egg production is constant and independent of prey abundance (Mills 1982). The shapes of the reproductive numerical responses determined in the lab-

oratory and the field (Mills 1982; Wright and Laing 1980) are identical although determined under quite different conditions. However, if egg laying were regulated solely by this response then eggs would be laid over a longer period. Therefore, it is relevant to ask: how do ladybirds manage to mainly oviposit in aphid colonies in the early stages of population development and so maximize their fitness?

In the present study, the reproductive numerical response was depressed by the presence of larvae. The larvae could have competed with the females for food when aphid numbers were low; however that is less likely when 10 aphids were provided and when 20 aphids were given there was enough food for both larvae and adults (Mills 1979). The lower numerical response is thus a consequence of an interaction between larvae and adult females, which does not involve competition for food. This is further supported by the observation that the females showed a marked reduction in the rate of oviposition in the presence of larvae of their own species but not of other species of aphidophagous ladybirds. This inhibition of oviposition, in the presence of one or two females or larvae of their own species, lasts for 3 h after which the oviposition rate increases dramatically, presumably because they are unable to refrain from egg laying any longer. The rate of encounter between larvae and females determines the extent of this inhibition.

The presence of conspecific larvae also provokes a high level of walking activity in females. The activity of predators is influenced both by their hunger (Holling 1966) and the presence of other predators. On encountering another individual of its own species, a searching predator may react by leaving the area (Hassell et al. 1976). As 50% of the prey provided to the females kept with larvae was uneaten, hunger does not seem to be the cause of the enhancement of activity reported here. The causal factor is more likely to be the presence of the larvae, which also affected egg laying.

Although it is unrealistic to equate laboratory and field conditions, the results of this study complement what is known of the natural history of ladybird beetles. The eggs and larvae are the two most vulnerable stages of these insects (Hodek 1973). The eggs of two-spot ladybirds, which are conspicuous and have a high nutritive value, are exposed to predators that forage on the leaves as do the ladybirds (Carter et al. 1984; Price et al. 1980). Of all the potential enemies, ladybird larvae are probably the most important threat, and several coccinellid species with a similar phenology can share the same habitat (Hodek 1973). Egg cannibalism in *A. bipunctata* is strongly density dependent (Mills 1982) and the later the oviposition in the ladybird *Harmonia axyridis* Pallas the more intense is non-sibling cannibalism (Osawa 1989). After hatching, competition between larvae could become severe and constitute the main risk. Avoiding oviposition in areas where larvae of the two-spot ladybird are already present reduces both the hazard of cannibalism and competition for food. The presence of ladybird larvae could also indicate that the aphid population is in a late stage of development. The reproductive behaviour of *A. bipunctata* leads it to oviposit near young

aphid colonies, which are unlikely to become extinct before the larvae complete their development. Gravid females of *A. bipunctata* appear to be able to assess the potential of an aphid population for supporting their offspring by responding to the presence of conspecific larvae. This form of habitat assessment is probably a common feature of insects that exploit resources that vary in abundance in time. Kan (1988a, b) reported habitat quality assessment by several species of hoverflies the larvae of which prey upon aphids. Syrphids are able to discriminate visually between apterous and alate aphids. A high proportion of winged aphids indicates that the colony is likely to be short-lived and as a consequence an unsuitable breeding place (Kan and Sasakawa 1986).

As in other predators, the spatial distribution of *A. bipunctata* results from their foraging and reproductive responses to patchily distributed prey. Much is known about their foraging behaviour but their reproductive responses have received less attention. It is generally assumed that the rate of egg production in ladybirds is a function of feeding rate (Gutierrez and Baumgaertner 1984). As pointed out by Evans and Dixon (1986), this is because the emphasis has been on the relationship between local rate of prey consumption and egg production. However, ladybirds are highly mobile predators moving from one patch of prey to another and apparently able to assess the quality and future potential of each patch for their larvae. As a consequence they tend to oviposit in particularly favourable aphid patches.

Ladybird beetles have been successfully used for the biological control of coccid pests (Bartlett 1978; Hodek 1973) whereas their role as biological control agents of aphids has been disappointing. Their reproductive behaviour might provide an explanation. The reproductive numerical response is confined to a narrow range of aphid densities and above approximately 10 aphids per 100 cm² egg production becomes independent of prey abundance as the ladybirds are satiated (Mills 1982). This in itself has a destabilizing effect on the predator-prey relationship and implies that ladybirds cannot control the abundance of prey populations once the prey exceeds the relatively low level at which the beetles are satiated (Crawley 1975; Dixon 1970; Wratten 1973). A second factor is egg cannibalism, which increases dramatically as egg density rises (Mills 1982). Whatever the adaptive value of egg cannibalism (Fox 1975), it is nevertheless wasteful in terms of reproductive effort. Thus it would be advantageous if females avoided ovipositing in locations where cannibalism and competition threaten the survival of their offspring. The laboratory experiments reported here support this hypothesis as females on the verge of oviposition will withhold eggs and are likely to leave an area after encountering larvae. As a consequence, the aggregative response of ladybirds to prey density is curtailed, which in addition to satiation at low prey densities accounts for their poor efficiency as biological control agents. Thus in addition to measuring a pest's distribution in space and the spatial response of natural enemies to pest density (Kareiva and Odell 1987; Kareiva 1990), there is a need to look at pest-enemy

interactions more in terms of what responses are likely to maximize the fitness of the natural enemy.

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