

Should aphidophagous ladybirds be reluctant to lay eggs in the presence of unsuitable prey?

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Abstract

The quality of different species of aphids as food for aphidophagous ladybird beetles varies greatly. The optimal oviposition theory predicts that a female should lay eggs preferentially in patches of suitable prey and should be reluctant to oviposit in patches of less suitable prey. A no-choice experiment was used to test whether aphids (Homoptera: Aphididae) of different suitability influence the oviposition behaviour of the two-spot ladybird beetle, *Adalia bipunctata* (L.) (Coleoptera: Coccinellidae). The results indicate that *A. bipunctata* females are not more reluctant to lay eggs in the presence of moderately suitable compared to highly suitable aphids. However, females laid fewer eggs in the presence of toxic aphids.

Introduction

Adults of aphidophagous ladybirds are likely to encounter different species of aphid when foraging for oviposition sites. Females are mobile and are able to move from one aphid patch to another. In this case, optimal oviposition theory predicts that females should lay eggs in those sites that are the most suitable for offspring development (see Mangel, 1987, 1989). It has been established for aphidophagous ladybirds that patch quality may depend on (1) the aphid species (Blackman, 1967; Mills, 1981; Olszak, 1986, 1988; Hauge et al., 1998; Kalushkov, 1998; Rana et al., 2002; Kalushkov & Hodek, 2004), (2) the number of aphids per unit area (Dixon, 1959), (3) the age of the aphid colony (Dixon, 2000), and (4) the presence of intra- or interspecific competitors/predators (Mills, 1982; Osawa, 1989, 1992, 1993; Evans, 1991; Burgio et al., 2002). All these factors may have been important in the evolution of the oviposition behaviour of aphidophagous ladybirds.

Previous experiments have demonstrated that the response of aphidophagous ladybirds to some of the factors mentioned corresponds to those predicted by

the optimal oviposition theory. For example, females avoid ovipositing in aphid colonies that are marked with an oviposition-detering pheromone (ODP) produced by conspecific larvae (Ruzicka, 1997, 2001; Doumbia et al., 1998; Yasuda et al., 2000; Fréchet et al., 2003). This behaviour is adaptive, as conspecific larvae readily eat ladybird eggs (Osawa, 1989, 1992).

However, the oviposition response of aphidophagous ladybirds to aphid quality is still unexplored. Many experiments have demonstrated that aphids are not all equally suitable for the larval growth or adult reproduction of a particular ladybird species (Blackman, 1967; Mills, 1981; Olszak, 1986, 1988; Hauge et al., 1998; Kalushkov, 1998; Rana et al., 2002; Kalushkov & Hodek, 2004). An experiment performed by Sengonca & Liu (1994) suggests that adults of the ladybird *Coccinella septempunctata* L. respond differently to the kairomones produced by different aphid species. This indicates that females might be able to discriminate between different aphid species. If this is the case, females should lay eggs more readily near suitable than moderately suitable or unsuitable aphids.

The link between adult preference for particular oviposition sites and subsequent larval performance has been extensively studied in phytophagous species (see for example Thompson, 1988; Berdegué et al., 1998; Harris et al., 2001; Craig & Ohgushi, 2002; Forister, 2004). However,

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only half of these studies established a link between oviposition preference and larval performance (Thompson, 1988; Mayhew, 2001). For example, Takeuchi et al. (2005) found that the phytophagous ladybird beetle *Epilachna admirabilis* Crotch shows no preference for *Trichosanthes cucumeroides* Maxim. over *Gynostemma pentaphyllum* Makino, even though the larvae performed better on the first plant species. However, there are few studies on the link between preference and performance in predators. The preference for some aphid species over others and its association with larval performance have been recorded for some aphidophagous syrphids (Sadeghi & Gilbert, 1999; Sadeghi, 2002) and chrysopids (Petersen & Hunter, 2002), but not for aphidophagous ladybirds.

The aim of this study was thus to evaluate whether ladybird females lay eggs more readily in the presence of a suitable than a moderately suitable or unsuitable aphid species. For the aphidophagous ladybird *Adalia bipunctata* L. (Coleoptera: Coccinellidae), the pea aphid, *Acyrtosiphon pisum* Harris, is generally regarded as suitable, and the black bean aphid, *Aphis fabae* Scopoli, raised on the same host plant, *Vicia faba* L., as moderately suitable for larval development (Blackman, 1967; Rana et al., 2002). The vetch aphid, *Megoura viciae* Buckton, is highly toxic to *A. bipunctata* (Blackman, 1967). In a first experiment, the oviposition response of *A. bipunctata* to the presence of these three aphids was studied. It is expected that *A. bipunctata* should be more reluctant to lay eggs in the presence of *A. fabae* than in the presence of *A. pisum*, and should avoid ovipositing in the presence of *M. viciae*. Moreover, according to the optimal oviposition theory, females should be less reluctant to lay eggs in the presence of unsuitable prey when mainly unsuitable prey is available in their habitat. Therefore, it is expected that *A. bipunctata* females will be less reluctant to lay eggs in the presence of *A. fabae* after being previously fed this species. This idea was tested in a second experiment.

Materials and methods

Insect cultures

The two-spot ladybird, *A. bipunctata*, used in these experiments came from a stock culture. Adults were reared at 18 ± 1 °C, L16:D8, in 5-l plastic boxes, that contained a piece of corrugated filter paper on which the females laid eggs. Ladybirds were fed an excess of pea aphids, *A. pisum*, three times a week. Two stems of broad bean, *V. faba*, were added to each box to improve the survival of the aphids and provide humidity.

Eggs were taken from the stock culture and incubated in 175 cm³ plastic boxes at 22 ± 1 °C during the day and 12.5 ± 1 °C at night, and L16:D8. After hatching, the larvae

were fed three times a week with an excess of *A. pisum* until pupation. The adults that emerged from these pupae were used in the experiments.

Females used in the experiments were standardized in order to minimize variations due to different rearing conditions. The adults were isolated within 24 h of their emergence from pupae. When their cuticles had hardened, they were sexed, and couples (one male and one female) were placed in a 90-mm Petri dish containing a piece of corrugated paper.

Couples were kept at 22 ± 1 °C during the day and 12.5 ± 1 °C at night, and L16:D8. Each day, couples were transferred to clean Petri dishes and fed an excess of pea aphids. The eggs laid were counted and removed daily. Ladybirds selected for the experiments had laid at least one egg batch per day in the last 5 days. In order to standardize hunger status and oviposition drive, females were deprived of food and males 16 h overnight before the beginning of the experiment.

Pea aphids, *A. pisum*, were reared in an air-conditioned chamber on broad beans, *V. faba*. Black bean aphids, *A. fabae*, and vetch aphid, *M. viciae*, were reared in a glasshouse also on *V. faba*.

First experiment

The first experiment was performed in order to determine the oviposition response of *A. bipunctata* females to three aphid species of different suitability. At the beginning of this experiment, each female was placed in a Petri dish with a piece of broad bean stem and about 50 aphids of mixed instars (from 1st instar to adult). The experiments consisted of either (1) females in the presence of *A. pisum* ($n = 17$), (2) females in the presence of *A. fabae* ($n = 17$), or (3) females in the presence of *M. viciae* ($n = 20$). Each female was assigned to only one treatment and then discarded. A no-choice experiment was chosen, as the aim of the experiment was to observe the oviposition response of *A. bipunctata* females to a given aphid species, which is the situation ladybirds are likely to encounter in the field. The number of eggs laid was recorded every hour for eight consecutive hours and then again after 24 h.

Second experiment

This experiment was performed in order to determine the influence of females' previous experience of unsuitable food on oviposition. Females were standardized as in the first experiment, with the exception that they were fed exclusively on *A. fabae* 4 days before the beginning of the experiment. Females were then placed either in the presence of (1) 50 *A. pisum* of mixed instars ($n = 18$) or (2) 50 *A. fabae* of mixed instars ($n = 18$). As in the first experiment, each female was assigned to only one treatment and then discarded.

Statistical analysis

The results were analysed using JMP IN® (SAS Institute, 2001). Even though the observations were made every hour, the results were analysed every 2 h as this was sufficient to determine a female's response. The proportions of females that had laid eggs and the proportion of females that died after 24 h were compared using a likelihood ratio test ($P < 0.05$). An ANOVA was used to compare the number of eggs laid after 8 and 24 h in the first experiment, only for those females that laid at least one egg. Where significant differences were found, a post hoc Tukey–Kramer HSD test was performed to determine the groups that differed. A two-way ANOVA was used to compare the number of eggs laid after 8 and 24 h in the second experiment.

Results

First experiment

Females in the three treatments showed the same propensity to lay eggs after 2 ($\chi^2 = 1.20$, d.f. = 2, $P = 0.55$), 4 ($\chi^2 = 5.15$, d.f. = 2, $P = 0.08$), 8 ($\chi^2 = 3.07$, d.f. = 2, $P = 0.22$), and 24 h ($\chi^2 = 0.87$, d.f. = 2, $P = 0.65$) (Figure 1). The only exception was observed after 6 h, when a significantly greater proportion of females laid eggs in the presence of *M. viciae* ($\chi^2 = 6.32$, d.f. = 2, $P = 0.04$).

The number of eggs laid by females were not different after 8 h ($F = 2.16$, d.f. = 2, $P = 0.14$) (Table 1). However, the numbers of eggs laid were statistically significant after 24 h ($F = 3.32$, d.f. = 2, $P = 0.05$). Females in the presence of *M. viciae* laid fewer eggs than females in the presence of *A. pisum* or *A. fabae* ($P < 0.05$). Significantly more females died when confined with *M. viciae* than with either *A. pisum* or *A. fabae* ($\chi^2 = 8.50$, d.f. = 2, $P = 0.01$) (Table 1).

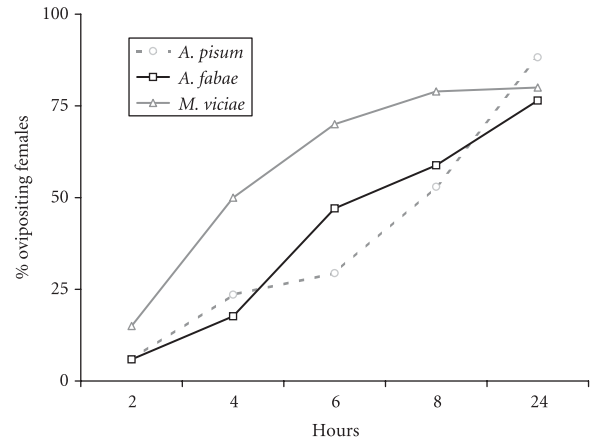


Figure 1 The percentage of *Adalia bipunctata* females that laid eggs in the presence of three different aphid species after 2, 4, 6, 8, and 24 h.

Second experiment

The results obtained with females previously fed with *A. fabae* were compared with those obtained in the first experiment. Similar proportions of females laid eggs after 2 ($\chi^2 < 0.01$, d.f. = 3, $P = 1.00$), 4 ($\chi^2 = 0.97$, d.f. = 3, $P = 0.81$), 6 ($\chi^2 = 2.25$, d.f. = 3, $P = 0.52$), 8 ($\chi^2 = 0.81$, d.f. = 3, $P = 0.85$), and 24 h ($\chi^2 = 2.41$, d.f. = 3, $P = 0.49$), regardless of the nature of the aphid previously fed on (Figure 2). The number of eggs laid after 8 and 24 h was similar in the different treatments (ANOVA: $F = 0.21$, d.f. = 3, $P = 0.89$; and $F = 0.38$, d.f. = 3, $P = 0.77$, respectively) (Table 1).

Discussion

Even though ladybirds can consume different aphid species, they should be more reluctant to lay eggs close to

Table 1 Mean number of eggs (\pm SE) laid by *Adalia bipunctata* females that oviposited after 8 and 24 h, and the percentage of mortality after 24 h in the presence of three different aphid species

	Previously fed on	Treatment	No. of eggs		Mortality (%)
			8 h	24 h	
Experiment 1	<i>A. pisum</i>	<i>A. pisum</i>	13.00 \pm 1.94 (n = 9)	14.40 \pm 1.33 (n = 15)	0
	<i>A. pisum</i>	<i>A. fabae</i>	11.40 \pm 1.69 (n = 10)	13.92 \pm 1.76 (n = 13)	0
	<i>A. pisum</i>	<i>M. viciae</i>	7.63 \pm 1.80 (n = 8)	9.63 \pm 1.38 (n = 16)	20
Experiment 2	<i>A. fabae</i>	<i>A. pisum</i>	13.10 \pm 1.80 (n = 10)	15.79 \pm 2.17 (n = 14)	0
	<i>A. fabae</i>	<i>A. fabae</i>	12.88 \pm 1.76 (n = 8)	16.58 \pm 2.56 (n = 12)	0

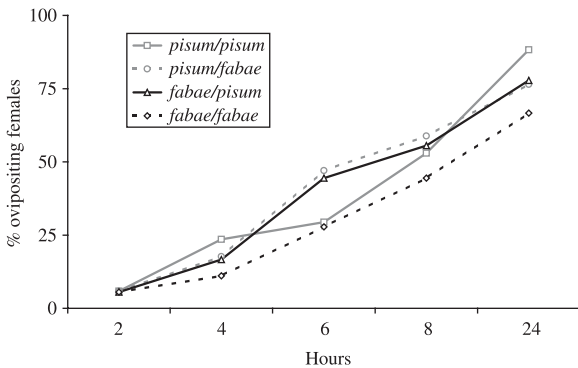


Figure 2 The percentage of *Adalia bipunctata* females previously fed on *Acyrtosiphon pisum* or *Aphis fabae* (first name in the box) that laid eggs in the presence of these two aphids (second name in the box) after 2, 4, 6, 8, and 24 h.

those species that are less suitable for the development of their offspring, especially those that are toxic. However, the results presented seem to indicate that *A. bipunctata* is not more reluctant to lay eggs in the presence of the moderately suitable *A. fabae*, or of the toxic *M. viciae*, than in the presence of the more suitable *A. pisum*. This is surprising, considering the high mortality of *A. bipunctata* larvae fed *A. fabae* (raised on *V. faba*) or *M. viciae* (Blackman, 1967; Rana et al., 2002). However, this lack of concordance has been repeatedly recorded for many phytophagous species (Mayhew, 2001).

The experimental design prevented females from leaving unsuitable patches. However, in a similar experiment, Fréchette et al. (2004) demonstrated that females are strongly affected by the presence of an oviposition-detering pheromone and refrain from ovipositing for some time. That is, although unable to leave unsuitable patches, one would expect the females similarly to have initially refrained from ovipositing.

According to Thompson (1988), four hypotheses can be put forward to explain the lack of an association between oviposition site choice and larval performance in insects: (1) The time hypothesis, which applies when a novel species enters a community. Natural selection may then take several generations to shape the new interactions. (2) The patch dynamics hypothesis, which states that the availability of suitable oviposition sites may be low due to variation in time and/or space in host abundance. A low abundance of good oviposition sites may thus result in a poor correspondence between adult preference and larval performance. (3) The parasite/grazer hypothesis, which distinguishes two types of insects: parasites that complete their development in a single host individual and grazers that must move between patches during the course of their larval development. The latter may be highly mobile,

which makes a strong preference for particular oviposition sites less important for the adults. (4) The enemy-free space hypothesis, which suggests that the presence of natural enemies may be as important (or more important) as food quality in shaping oviposition behaviour. Natural selection could thus have favoured the preference for oviposition sites that are free of enemies over those of high food quality. These hypotheses were originally developed to account for the oviposition preferences of phytophagous insects, but as Sadeghi & Gilbert (1999) pointed out, the selection pressures affecting oviposition in predators and phytophagous insects are likely to be similar.

The ladybird *A. bipunctata* and the aphids *A. fabae* and *M. viciae* are all indigenous species in Europe. Hence, the time hypothesis (the lack of time for adaptive evolution) cannot explain the results presented in this paper. Similarly, the parasite/grazer hypothesis does not apply because 1st instar ladybird larvae have to find aphid prey quickly (Banks, 1957) and are not very mobile (Kawai, 1976). Thus, ladybird eggs are generally laid near aphid colonies.

Thompson's other two hypotheses must be given more consideration. The patch dynamics hypothesis, which stresses the importance of patch availability, may account for the lack of association recorded in this study. Although ladybirds lay eggs over a period of months, aphid abundance can change very rapidly. At different times of a year, different aphid species are available. A good-quality aphid may be very abundant at one time and then scarce a few weeks later. Moreover, the abundance of an aphid species may vary considerably from one year to another. Thus, it may not be advantageous for ladybirds to discriminate precisely between different aphid species. This could explain why *A. bipunctata* eggs are regularly observed in natural colonies of *A. fabae* in England (Banks, 1955, 1956) despite the low quality of this aphid for the larval development of this ladybird.

The enemy-free space hypothesis should also be considered, although the design of the experiment did not test this hypothesis. Ladybird larvae and eggs are highly susceptible to cannibalism and intraguild predation (Osawa, 1989, 1992; Lucas et al., 1997, 1998). For this reason, females avoid laying eggs on plants where they detect cues indicating the presence of conspecific larvae (Fréchette et al., 2003). Even though not tested in the field, they may also respond to cues indicating the presence of intraguild predators (Ruzicka, 2001). Griffin & Yeargan (2002a, 2002b) found that the ladybird *Coleomegilla maculata* (DeGeer) prefers to lay eggs on certain plants regardless of the presence or the absence of prey; the preferred plants are those with glandular trichomes, which lower the risk of egg predation and cannibalism. These two examples indicate that the risk of predation may be more

important in determining the oviposition behaviour of ladybirds than the presence or quality of food. That is, a patch of prey that is free of natural enemies may be preferred regardless of the aphid species present. The patch dynamics and enemy-free space hypotheses are not mutually exclusive, and may provide complementary explanations.

An alternative explanation for ovipositing in the presence of *A. fabae* could be that the ladybirds used in this experiment perform better on *A. fabae* than those used in the experiments of Blackman (1967) and Rana et al. (2002). Soares et al. (2003) demonstrated that the suitability of two aphid species was different for two phenotypes of the ladybird *Harmonia axyridis* Pallas. *Adalia bipunctata* is also polymorphic; however, the phenotype of the females was not taken into consideration in our experiment, or those of Blackman (1967) and Rana et al. (2002). Nevertheless, populations may be adapted to local conditions and thus perform differently on a given diet. Rana et al. (2002) demonstrated that when fed for many generations on *A. fabae*, *A. bipunctata* eventually performed as well on this prey as on *A. pisum*. Preliminary results for ladybirds from our stock culture indicate that *A. bipunctata* larvae do not suffer the same high mortality when fed *A. fabae* as previously observed by other authors (J-L Hemptinne, unpubl.). If this is the case, then it is possible that the ladybirds we used may be better adapted to feeding on *A. fabae* and thus less likely to refrain from ovipositing in the presence of this aphid. However, although this may account for the results obtained using *A. fabae*, it cannot account for those obtained using *M. viciae*. *Adalia bipunctata* females were not reluctant to lay eggs in the presence of this aphid, although it is highly toxic; 20% of the females were dead after being confined for 24 h with this aphid.

Yet another hypothesis is that the ladybirds first select the habitat (Ferran & Dixon, 1993). *Adalia bipunctata* is usually considered as a shrub- and tree-dwelling ladybird even though it may also colonize other types of vegetation when prey is abundant (Honek & Rejmanek, 1982; Honek, 1985). If this was the case, then it would make it very unlikely that this species would encounter aphid species associated with low vegetation, such as *M. viciae*. A low probability of encounter in the field could account for the results obtained in this study with this aphid.

Egas & Sabelis (2001) have demonstrated that the spider mite, *Tetranychus urticae* Koch, could learn to choose a good host and avoid a bad one when ovipositing. Spider mites that have never experienced a bad host often first accept it as a good host. Our results indicate that *A. bipunctata* fed *A. fabae* for 4 days before the experiment were not more reluctant to oviposit in the presence of this aphid than those that had no previous experience of this aphid. That is, if *A. fabae* is really less suitable than

A. pisum for the population of *A. bipunctata* we used, there is no evidence of associative learning affecting oviposition in this ladybird species.

The presence of aphids or aphid honeydew is a cue for oviposition for aphidophagous ladybirds (Evans & Dixon, 1986). The results of our experiments seem to suggest that the presence of aphids or aphid cues, regardless of whether the species is suitable or not for larval development, is enough to stimulate oviposition in *A. bipunctata*. The results presented in this paper raise further questions about the assessment of patch quality for oviposition by aphidophagous ladybirds. Further field and laboratory experiments are needed to resolve which of the components of patch quality are important in a ladybird's decision to oviposit.

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