

Age and experience influence patch assessment for oviposition by an insect predator

BRUNO FRECHETTE,¹ ANTHONY F. G. DIXON,² CLAUDE ALAUZET¹ and JEAN-LOUIS HEMPTINNE³

¹Université Paul Sabatier, Laboratoire d'écologie terrestre, Toulouse, France, ²School of Biological Sciences, University of East Anglia, Norwich, U.K. and ³Ecole Nationale de Formation Agronomique, Laboratoire d'Agro-écologie, Auzeville, France

Abstract. 1. Dynamic models of optimal foraging predict that an animal's decision to accept or reject a patch depends not only on the environment and patch quality, but also on its internal state. Previous experiments have shown that the two-spot ladybird beetle, *Adalia bipunctata* (L.), is reluctant to lay eggs in a patch of prey contaminated by the oviposition-detering pheromone produced by conspecific larvae.

2. An experiment was conducted to test whether the internal state of an *A. bipunctata* female affects its oviposition response to oviposition-detering pheromone. Firstly, the oviposition response to oviposition-detering pheromone of young and old females was compared. Secondly, the oviposition response to oviposition-detering pheromone of females previously exposed continuously to oviposition-detering pheromone was compared with that of females of the same age but with no previous experience of oviposition-detering pheromone.

3. Old females and females with previous experience of oviposition-detering pheromone were less reluctant to lay eggs in the presence of oviposition-detering pheromone than young and naive females. These results are consistent with the predictions of optimal foraging theory.

Key words. *Adalia bipunctata*, Coccinellidae, dynamic models, larval tracks, optimal foraging, oviposition-detering pheromone, state dependent.

Introduction

The optimal foraging theory developed by Charnov (1976) for a predator that investigates patches of food is also applicable to insects seeking a suitable site to lay eggs (Mangel, 1987). A female will optimise her fitness by choosing oviposition sites that contribute more to lifetime fitness, considering the cost in energy and time of moving from one patch to another and of evaluating patch quality. According to Charnov (1976), a female should accept a patch if its quality is superior to the mean patch quality. Many observations support this theory (e.g. Pallini *et al.*, 1998).

A female seeking an oviposition site is also expected to forage optimally. When in a patch, a female has to choose between an immediate increment in fitness by laying eggs in that patch or taking a chance on future expected fitness by leaving that patch (Mangel, 1987). This assumes that a forager makes its decisions based on its knowledge or experience of the environment. Such behavioural responses have mainly been studied in various species of parasitoids (Poolman Simons *et al.*, 1992; Visser *et al.*, 1992; Michaud, 1996; Li *et al.*, 1997; Reznik *et al.*, 1997; Hoffmeister *et al.*, 2000; Keasar *et al.*, 2001; Morris & Fellowes, 2002). Usually, these studies compare either (1) the oviposition responses of females that have previously competed, or not, for oviposition sites, or (2) the oviposition response of females that visit a sequence of more or less good quality patches. Results generally tend to confirm the prediction of optimal foraging theory, i.e. females are less selective after experiencing competition or visiting poor quality patches. For example, *Leptopilina heterotoma* (Thomson) females

Correspondence: Jean-Louis Hemptinne, Ecole Nationale de Formation Agronomique, Department ARGE, B.P. 87, 31326 Castanet-Tolosan Cedex, France. E-mail: jean-louis.hemptinne@educagri.fr

that have just visited a patch where most of the hosts are already parasitised spend more time in the next patch and are more likely to superparasitise than those that previously visited a patch where hosts were mainly unparasitised (Visser *et al.*, 1992). Similarly, the parasitoid *Trichogramma thalense* Pinto and Oatman modifies its oviposition rate in response to past experience of host quality (Kearse *et al.*, 2001).

However, to the authors knowledge, this kind of experiment has been done only once using predators that previously visited high or low prey density patches (Nakashima & Hirose, 2003), but never with predators with previous experience of the presence of conspecifics. Studying predators is of fundamental importance since they differ from parasitoids in two important respects: (a) eggs are not laid in or on the prey and may be deposited far from prey and (b) the larvae of predators have to pursue and subdue their prey.

The first optimal foraging models (e.g. Charnov, 1976) were static and assumed that a forager's decisions depended only on extrinsic factors, i.e. patch quality, patch availability, general quality of the environment, etc. Then dynamic models were developed that stressed the importance of intrinsic factors like age, experience, energy reserves, and egg load in decision making by foragers (Mangel & Clark, 1986; Mangel, 1987, 1989). Age, through time limitation, should be an important factor determining a forager's decision; when an organism is close to the end of its life it may be more advantageous for it to accept a poor quality oviposition site than it is for a young organism (Mangel, 1989). This decline in selectivity with age has some empirical support. For example, young aphidophagous hoverflies, *Episyrphus balteatus* (Degeer) and *Syrphus ribesii* (L.), show a marked hierarchical preference for ovipositing with particular species of aphids, while old females are less selective (Sadeghi & Gilbert, 2000). Weisser (1994) also demonstrated that as the parasitoid *Lysiphlebus cardui* Marshall ages it becomes less selective about the age of the aphids it parasitises. However, in the field, Heimpel *et al.* (1996) found no evidence of age affecting the oviposition behaviour of the parasitoid *Aphytis aonidiae* (Mercet).

Aphidophagous coccinellids are a good model for studying optimal oviposition behaviour in insect predators. Females usually lay their eggs near aphid colonies (Dixon, 1959; Evans & Dixon, 1986), which can be viewed as patches of prey. For ladybirds patch quality may depend upon the aphid species (Blackman, 1967; Hauge *et al.*, 1998; Kalushkov, 1998; Rana *et al.*, 2002), the number of aphids per unit area (Dixon, 1959), the age of the colony (Dixon, 2000), and the presence of intra- or interspecific competitors (Mills, 1982; Osawa, 1989, 1993; Burgio *et al.*, 2002). Females avoid laying eggs in patches where there are conspecific larval tracks, which contain an oviposition-detering pheromone (Ruzicka, 1997; Doumbia *et al.*, 1998; Yasuda *et al.*, 2000; Ruzicka, 2001; Fréchette *et al.*, 2003). The larval tracks of *Adalia bipunctata* (L.) contain at least 40 components, most of which are alkanes (Hemphlin *et al.*, 2001), and these tracks are known to deter oviposition.

Since alkanes readily spread on the hydrophobic cuticle of plants and are not easily oxidised, they could constitute a large and long lasting cue. The advantage of responding to oviposition-detering pheromone is obvious when ladybirds are relatively uncommon; by avoiding aphid colonies that are already exploited, females lower the risk of their offspring being subject to competition and cannibalism. However, optimal foraging theory indicates that a ladybird's response to oviposition-detering pheromone should not be fixed, but flexible and dependent on the quality of the environment and/or physiological state of the female.

When ladybirds are abundant relative to their aphid prey it is likely that many colonies of aphids will contain ladybird larvae. Under these conditions females should alter their response to oviposition-detering pheromone. If they do not lay eggs in colonies marked with oviposition-detering pheromone they run the risk of having zero fitness. In addition, whatever the longevity of adult ladybirds in the field, the average life expectancy of a young female is longer than that of an old female. Thus, an old female should more readily accept an oviposition site marked with oviposition-detering pheromone than a young female because the older female has less chance of finding another patch of prey.

The objective of this study was to evaluate the effect of age and experience on the oviposition response of gravid females of *A. bipunctata* to oviposition-detering pheromone.

Methods

Ladybird culture

The two-spot ladybird, *Adalia bipunctata* (L.), used in this study came from a stock culture. This consisted of adults reared at $18 \pm 1^\circ\text{C}$, LD 16:8 h, in 5-litre plastic boxes, which contained a piece of corrugated filter paper on which the females laid eggs. Three times a week the ladybirds were fed an excess of pea aphids, *Acyrtosiphon pisum* Harris. Two stems of broad bean, *Vicia faba* L., were added to each box to improve the survival of the aphids.

For the experiments, eggs were taken from the stock culture and incubated in 175-cm³ plastic boxes under the same conditions as the stock culture. After hatching larvae were fed three times a week with an excess of pea aphids until pupation. Freshly emerged adults were used for the experiments.

Oviposition-detering pheromone-contaminated filter paper

Oviposition-detering pheromone-contaminated filter papers were required for both experiments. Contaminated filter papers were produced by placing a 90-mm diameter Whatman[®] filter paper in the lids of 90-mm diameter Petri dishes in which five fourth-instar *A. bipunctata* larvae were kept with an excess of pea aphids for 24 h. After 24 h, the larvae and aphids were removed and the filter paper was

brushed to remove faeces, surviving aphids, and aphid remains. As Evans and Dixon (1986) demonstrated that aphid remains and honeydew do not refrain ladybird oviposition, and even enhance it in the absence of aphids, control filter papers were clean filter papers.

Standardisation of females

Females were standardised in order to minimise variations due to the different rearing conditions. The adults were isolated within 24 h of their emergence from pupae. When their cuticles had hardened, they were sexed using Kovar's (1996) method and couples, consisting of a male and a female, were placed in a 90-mm Petri dish containing a piece of corrugated paper and kept at $20^{\circ}\text{C} \pm 1^{\circ}\text{C}$, LD 16:8 h. 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 in the previous 5 days. In order to standardise hunger and oviposition drive, females were deprived of food and males 16 h overnight before the beginning of the experiment.

First experiment – age

In this experiment the oviposition response of *young* and *old* females in the presence or absence of oviposition-detering pheromone was compared. *Young* females were those that commenced egg-laying less than 10 days previously and *old* females those that had laid eggs for more than 30 days.

At the beginning of this experiment each female was placed into a Petri dish with a piece of bean stem and about 50 aphids of mixed instar. These females were randomly subjected to one of four treatments: (1) *young* females with control filter paper, (2) *young* females with oviposition-detering pheromone-contaminated filter paper, (3) *old* females with control filter paper, and (4) *old* females with oviposition-detering pheromone-contaminated filter paper. There were 20 replicates of each treatments.

The ladybirds were observed continuously for the first 2 h, then every hour for a further 6 h and finally after 24 h. At each of these observations it was noted whether they had laid eggs and how many.

In addition, at the beginning of the experiment and every hour for up to 8 h, the behaviour of the *young* and *old* females in the control treatments was observed to determine the impact of age on activity levels. Every minute, for 5 min, it was noted whether the beetles were *walking*. This resulted in a total of 45 records for each beetle.

Second experiment – experience

In this experiment the oviposition responses to oviposition-detering pheromone of females that had previously

been continuously kept from the second day of their adult life in Petri dishes with filter paper contaminated with oviposition-detering pheromone for 15.5 ± 0.8 days ($n=45$; *experienced* females) were compared with those kept in Petri dishes with control filter paper for the same period (*naive* females). As a consequence, the females selected for this experiment were all of the same age and had laid between five and 15 clutches of eggs.

At the beginning of this experiment, females that regularly oviposited were each placed in a 90-mm Petri dish with filter paper, a section of bean stem and about 50 pea aphids. There were four treatments: (1) *experienced* females with oviposition-detering pheromone-contaminated filter paper, (2) *experienced* females with control filter paper, (3) *naive* females with oviposition-detering pheromone-contaminated filter paper, and (4) *naive* females with control filter paper. There were 25 replicates for treatments 1, 3, and 4 and 24 for treatment 2.

The oviposition responses of the females were recorded using the same method as in the first experiment.

Statistical analyses

The results were analysed using JMP IN[®] (SAS Institute, 2001). The proportions of females that laid eggs were compared using a χ^2 test. When the χ^2 test detected a significant difference ($P < 0.05$), a Tukey-type multiple comparison test was computed by hand following Zar (1996) in order to determine the groups that differed.

An ANOVA was used to compare the numbers of eggs laid after 8 and 24 h only among females that did oviposit. Data were normalised by a squared root transformation (Shapiro–Wilk test: $P > 0.05$).

In the first experiment, the percentages of occasions on which young and old adults were observed *walking* in the Petri dishes with control filter paper were arcsine transformed in order to normalise the distribution and stabilise the variance. Transformed values were then compared using an ANOVA.

Results

First experiment – age

Only a few females laid eggs in the first two hours of the experiment. The differences recorded at that time between the four treatments were not significant (Fig. 1; $\chi^2_{2h} = 6.316$, d.f. = 3, $P = 0.097$). After 4, 6, and 8 h proportions were not equal (Fig. 1; $\chi^2_{4h} = 9.592$, d.f. = 3, $P = 0.022$; $\chi^2_{6h} = 10.980$, d.f. = 3, $P = 0.012$; $\chi^2_{8h} = 13.867$, d.f. = 3, $P = 0.003$). Significantly more *young* females kept on control filter paper laid eggs than *young* females in the presence of oviposition-detering pheromone ($P < 0.05$). However, *old* females oviposited as readily in Petri dishes with paper contaminated with oviposition-detering pheromone as in

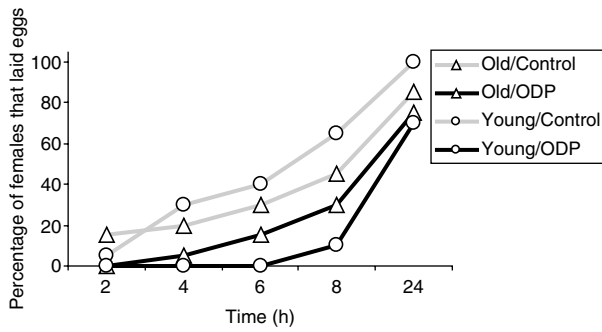


Fig. 1. The percentage of *old* (Δ) and *young* (\circ) females that laid eggs in the oviposition-detering pheromone (ODP) (black lines) and the control treatments (grey lines) after 2, 4, 6, 8, and 24 h.

those with control paper ($P > 0.05$). Also, even if significant differences were not detected, *old* females tended to lay more readily in the presence of oviposition-detering pheromone than *young* females ($P > 0.05$). The *old* females laid eggs as frequently as the *young* females on control filter paper ($P > 0.05$). At the end of the experiment, the percentage of females that had laid eggs was similar in the four treatments (Fig. 1; $\chi^2_{24h} = 7.273$, d.f. = 3, $P = 0.064$). However, all of the *young* females in the control treatment laid eggs, while only 70% of those in the oviposition-detering pheromone treatment did. Data collected in the rearing unit on two different dates when the ladybirds were not subjected to the treatments showed that the percentage of females that oviposited in a 24-h cycle was respectively, 92% ($n = 25$) and 90.5% ($n = 21$). These percentages were close to those of the control treatments.

Among females that oviposited, neither age nor treatment had an influence on the number of eggs laid after 8 h (Table 1; ANOVA: $F_{3,26} = 0.625$, $P = 0.606$) and 24 h (ANOVA: $F_{3,62} = 0.412$, $P = 0.745$). That is, females do not withhold eggs once oviposition started even in unfavourable conditions.

The *young* females on control paper spent a greater percentage of their time walking than the *old* females in similar condition (Table 2; ANOVA: $F_1 = 22.289$, $P < 0.001$). That is, *young* females were more active than the *old* females in the control treatments.

Table 1. The mean numbers of eggs laid (\pm SE) by young and old females of *Adalia bipunctata* after 8 and 24 h in a Petri dish with a control filter paper or with a filter paper contaminated with oviposition-detering pheromone (ODP).

Treatment	8 h		24 h	
	<i>n</i>	No. of eggs	<i>n</i>	No. of eggs
Young/Control	13	9.23 \pm 1.34	20	12.00 \pm 0.93
Young/ODP	2	13.00 \pm 6.00	14	10.79 \pm 1.90
Old/Control	9	10.44 \pm 0.87	17	11.47 \pm 1.37
Old/ODP	6	14.00 \pm 3.73	15	13.33 \pm 2.27

Table 2. The mean percentage (\pm SE) of *young* and *old* *Adalia bipunctata* females observed walking in the control treatment.

Treatment	<i>n</i>	Walking
Young/Control	45	57.3 \pm 2.7
Old/Control	45	35.5 \pm 3.7

Second experiment – experience

The percentage of females that laid eggs 2 and 4 h after the beginning of the experiment were not significantly different (Fig. 2; $\chi^2_{2h} = 3.939$, d.f. = 3, $P = 0.268$; $\chi^2_{4h} = 3.152$, d.f. = 3, $P = 0.369$). After 6 and 8 h, significant differences appeared between the four treatments (Fig. 2; $\chi^2_{6h} = 11.135$, d.f. = 3, $P = 0.011$; $\chi^2_{8h} = 15.215$, d.f. = 3, $P = 0.002$). Fewer *naive* females laid eggs on filter paper contaminated with oviposition-detering pheromone than on control paper ($P < 0.01$). On the contrary, the presence or the absence of oviposition-detering pheromone did not influence the *experienced* females ($P > 0.05$). *Experienced* females laid eggs as frequently as the *naive* females in the control treatment ($P > 0.05$). However, even though a greater proportion of *experienced* females laid eggs on filter paper contaminated with oviposition-detering pheromone than *naive* females, the difference was not statistically different ($P > 0.05$). After 24 h, many of the *naive* females had laid eggs in the presence of oviposition-detering pheromone. As a consequence, the percentages of females laying eggs in the four treatments were no more significantly different (Fig. 2; $\chi^2_{24h} = 3.475$, d.f. = 3, $P = 0.324$).

As for the first experiment, neither experience nor treatment had an influence on the number of eggs laid after 8 h among the females that oviposited (Table 3; ANOVA: $F_{3,39} = 0.474$, $P = 0.702$) and 24 h (ANOVA: $F_{3,81} = 1.989$, $P = 0.316$).

Discussion

Dynamic optimal foraging models predict that female insects should modify their egg-laying behaviour in response to both intrinsic and extrinsic factors. For a

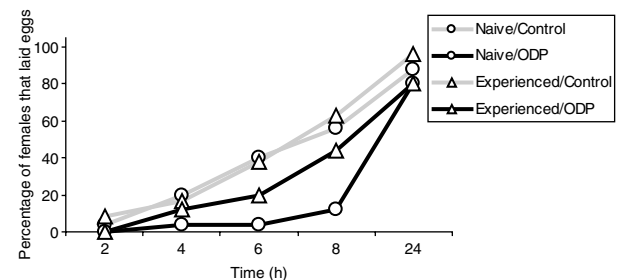


Fig. 2. The percentage of *experienced* (Δ) and *naive* (\circ) females that laid eggs in the oviposition-detering pheromone (ODP) (black lines) and the control treatments (grey lines) after 2, 4, 6, 8, and 24 h.

Table 3. The mean numbers (\pm SE) of eggs laid by naive and experienced females of *Adalia bipunctata* after 8 and 24 h in a Petri dish with a control filter paper or a filter paper contaminated with oviposition-detering pheromone (ODP).

Treatment	8 h		24 h	
	<i>n</i>	No. of eggs	<i>n</i>	No. of eggs
Naive/Control	14	8.71 \pm 1.15	22	17.41 \pm 2.03
Naive/ODP	3	8.33 \pm 0.88	20	14.85 \pm 1.85
Exp./Control	15	12.00 \pm 2.28	23	16.35 \pm 1.95
Exp./ODP	11	12.64 \pm 3.06	20	13.15 \pm 2.32

predaceous insect exploiting aphid colonies, the relative quality of patches of prey and the predator's physiological state may influence the decision to lay eggs.

This study demonstrates that females of the aphidophagous ladybird *A. bipunctata* were less selective when they were old or when they had previously experienced poor quality patches. This accords with the predictions of dynamic models of optimal foraging (Mangel, 1989). Even though one should be cautious when extrapolating from laboratory results, this study indicates that female behaviour is not fixed.

Old females more readily laid eggs in the presence of oviposition-detering pheromone than young females. What caused this change in behaviour with age was not determined. It could be due to a loss of chemoreceptors' efficacy associated with senescence; however, whatever the cause, the consequence is adaptive. It can be assumed that the probability of death increases with age (e.g. Tatar *et al.*, 1993) so that old females have theoretically less time to complete oviposition than young females and should thus be less selective (Mangel, 1989).

Since ladybirds seem to "age" more slowly in the field than in the laboratory, the above change in the behaviour of females is likely to occur at a more advanced age; however the result is likely to be the same. Females in the laboratory are usually well fed and oviposit daily and it is known that reproduction induces ageing in insects (Tatar *et al.*, 1993; Dixon, 2000). The mortality rate of the individuals that survived more than 3 months increased markedly after that time. That is, after 30 days of laying eggs the ladybirds were clearly ageing.

The experimental females also became less active as they aged. Dixon and Agarwala (2002) observed that the speed of movement of *Harmonia axyridis* Pallas declines with age. This is one more reason why ladybirds should become less selective as they age. That is, with increase in age the beetles take longer to locate another patch of prey.

A female that finds most patches of prey are already being attacked by conspecifics should more readily accept their presence and oviposit since it is probable that she will not find a patch that is not being attacked. This study demonstrates that females raised in the presence of a signal indicating the presence of conspecific larvae tend to ignore it. It is believed that this is the first time that this kind of

experiment has been carried out with a predator, as opposed to a parasitoid species. This reveals that the adjustment of the oviposition behaviour in response to the quality of the environment, often described for parasitoid species, also occurs in an aphid predator.

Finally, even if females are reluctant to lay eggs in the presence of oviposition-detering pheromone, when they do so they do not alter their clutch size. That is, the oviposition-detering pheromone only influences the decision to lay eggs or not.

Only two of the many factors that may influence a female's acceptance of an oviposition site contaminated with oviposition-detering pheromone were explored here. The species of aphid, the age, and the density of the aphid colony are other factors affecting patch quality (Dixon, 2000). The egg load of the female may also alter her behaviour, as observed in other organisms (Collins & Dixon, 1986; Mikenberg *et al.*, 1992; Heimpel *et al.*, 1996; van Randen & Roitberg, 1996).

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