

Do female coleopteran parasitoids enhance their reproductive success by selecting high-quality oviposition sites?

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Summary

1. Female parasitoids that lay their eggs away from potential host insects are supposed to have only a minor influence on the fitness of their own progeny, as they do not select and evaluate directly the quality of hosts for their offspring. *Aleochara bilineata* Gyll. (Coleoptera: Staphylinidae) females oviposit near to cabbage plants infested by larvae of *Delia radicum* L. (Diptera: Anthomyiidae). Once the mobile *A. bilineata* larva emerges from the egg, it must then search the soil to find and select a suitable fly pupa. The beetle larvae have a limited time to found pupae and can only parasitize one host pupa during their lifetime. Moreover, because *A. bilineata* is a solitary parasitoid whether or not the host pupa is parasitized, has a strong influence on the successful development of the beetle larva.

2. We studied the oviposition behaviour of *A. bilineata* females in laboratory experiments in which females could choose between a range of several oviposition sites.

3. Our results reveal that *A. bilineata* females, like hymenopteran parasitoid females, show an adaptive oviposition behaviour in response to the quality of the oviposition site. The female beetles adapt their oviposition decisions and their clutch size based on information associated with the presence of a host. Furthermore, our results reveal that the *Aleochara* females can discriminate between specific cues related to the stage and parasitization status of the host. Such behaviours may greatly enhance the parasitization success of the larvae, and thereby female fitness.

Key-words: parasitoids, oviposition behaviour, fitness, *Aleochara*.

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Introduction

In hymenopteran parasitoids, the fitness of females is essentially related to their ability to find hosts and evaluate their quality. In such parasitoids, host location is based on infochemicals, emitted by the plant, the host insect or derived from the activity of the host (Alborn *et al.* 1997; Paré & Tumlinson 1997). These signals can inform the females about the presence, identity and availability of hosts (Vet & Dicke 1992; De Moraes *et al.* 1998). After locating a host, the female hymenopteran parasitoid must determine its suitability before ovipositing. The suitability of a given host depends on the size of the host insect, its stage of development and

whether or not it is already parasitized (i.e. parasitization status) (see Godfray 1994 for a review). In solitary hymenopteran parasitoids, the host parasitization status plays an essential role in offspring survival, as only one larva can successfully develop per host. Accordingly, females that can discriminate between unparasitized and parasitized hosts (Roitberg & Mangel 1988) should avoid superparasitism when unparasitized hosts are common (Bakker *et al.* 1985; Harvey, Marris & Hubbard 1987; Janssen 1989; van Alphen & Visser 1990; but see also Visser, van Alphen & Nell 1990; Visser, van Alphen & Hemerik 1992; Visser 1995).

Although more information is becoming available on the selection of hosts by hymenopteran parasitoids, little is known about how coleopteran parasitoids select their host insects.

In coleopteran parasitoids, the location of hosts by larvae is the most common mode of infestation (Eggleton & Belshaw 1993). The female beetles lay

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eggs where there is general evidence of hosts (Godfray 1994). However, the precise finding and selection of hosts is performed only by the mobile first instar larva, which starts to search for hosts immediately after hatching. Therefore, in comparison with most hymenopteran parasitoids, coleopteran parasitoids are considered to have only a minor influence on the parasitism success and fitness of their progeny, as they do not directly select and evaluate host suitability (Godfray 1994).

In *Aleochara* species (Coleoptera: Staphylinidae), adults are predators of dipteran eggs while larvae are parasitoids of dipteran pupae (Wadsworth 1915; Fuldner 1960; Maus, Mittman & Peschke 1998; Ferreira de Almeida & Pires do Prado 1999). In Brittany (west of France) *Aleochara bilineata* Gyll. is one of the three major parasitoids of *Delia radicum* L. (Diptera: Anthomyiidae), the cabbage root fly, in cole-crop fields (Brunel & Fournet 1996). *Delia radicum* eggs and larvae are often aggregated, resulting in a patchy distribution of hosts (Mukerji & Harcourt 1970). After hatching, *A. bilineata* larvae actively search for hosts but have only a limited time to find, evaluate and parasitize a pupa. In addition, they are strongly 'egg-limited' as they can only parasitize one host during their lifetime (Fuldner 1960).

As in hymenopteran parasitoids, the successful development of *A. bilineata* larvae depends on host quality (i.e. size, development stage and parasitization status) (Ahlström-Olsson 1994; Royer *et al.* 1999). As *A. bilineata* is a solitary parasitoid, whenever more than one larva penetrates a single host puparia, the larvae will fight until only one survives (Fuldner 1960), but sometimes both die (Fournet *et al.* 1999). Thus, as superparasitism is potentially lethal, the larvae, when given the choice, always prefer to enter unparasitized host puparia (Fournet *et al.* 1999; Royer *et al.* 1999). In spite of their ability to detect the host parasitization status, the larvae become less selective and penetrate already-parasitized hosts when they run out of time (Royer *et al.* 1999). This suggests that short host-searching time may favour selection of high quality hosts (i.e. hosts that maximize survival and fitness of the progeny) while long searching-time may favour parasitization of hosts of very different quality.

In the present study, we investigated whether *A. bilineata* females can select oviposition sites that ensure a short searching-time and better quality hosts for their larvae. We addressed this question by studying how females distribute their eggs in their foraging environment with respect to the presence of stimuli from host plant, host eggs and host pupae.

Materials and methods

REARING

Colonies of *D. radicum* and *A. bilineata* were established using field-collected *D. radicum* pupae from La Rimbaudais, Brittany, France, and were maintained

at 20 °C, 65% relative humidity (r.h.) 18L : 6D. Adults of *D. radicum* were provided with a source of water, milk powder, sugar, as well as two half turnips placed on moist filter paper in plastic cups to serve as oviposition sites. The turnips were changed twice weekly and *D. radicum* larvae were allowed to develop in the turnips until pupation.

Males and females of *A. bilineata* and *A. bipustulata* were reared according to the method described by van Keymeulen & Herdvelde (1982), and were provided with minced beef as a source of food. Eggs were incubated on damp cloth in Petri dishes (80–90% r.h.) and larvae were reared on *D. radicum* pupae.

EXPERIMENTAL SET-UP

All experiments were carried out in a 42-cm square arena that was 7 cm high. This test arena contained moistened sand (2 cm), was covered with a transparent lid and was kept under constant conditions (20 °C, 65% r.h., 18L : 6D). Each *Aleochara* female was used for one 48-h test period only. Females were 8–20 days old, mated and had no contact with any host stage (egg, larvae or pupae, other than those from which they emerged) before the experiments. In each experiment, the beetle eggs were extracted from the sand by flotation in a saturated salt solution, filtered on a piece of mesh screen (150 × 150 µm) and counted.

OVIPOSITION SITES TESTED

Oviposition sites consisted of a plastic cup (6 × 6 cm or Ø 14.2 cm) and contained moist sand and half a turnip 'root'. To investigate how female beetles distribute their eggs in their foraging environment and to determine what precise host and plant cues they use to evaluate oviposition sites quality, the following oviposition sites were used in the experiments described in the next section:

- *Undamaged plant.* One uninfested half turnip.
- *Undamaged plant with D. radicum eggs.* One uninfested half turnip surrounded with *D. radicum* eggs.
- *Damaged plant.* One half turnip infested with *D. radicum* larvae until they reached their third instar. These larvae were removed from the root immediately prior to the test.
- *Crushed damaged plant.* After removal of *D. radicum* larvae, part of a 'damaged plant' was crushed in a mortar immediately prior to the test. In paired tests, comparisons were made between 'damaged plant' and 'crushed damaged plant', obtained from the same infested turnip.
- *Damaged plant with unparasitized host pupae.* One turnip was infested with 30 *D. radicum* larvae. These were allowed to develop and pupate in the sand beneath the root. In paired comparisons between this treatment and either, 'damaged plant' or 'crushed damaged plant', the two treatments again came from the same infested turnip.

- *Damaged plant with parasitized host pupae.* One turnip was treated as described previously for 'Damaged plant with unparasitized host pupae'. Four days before the beginning of the test, 30 *A. bilineata* first instar larvae were deposited on the sand to parasitize the available pupae. In paired comparisons between this treatment and 'damaged plants with unparasitized host pupae', the test halves came from the same infested turnip.
- *Naturally buried hosts.* Twenty *D. radicum* larvae were allowed to pupate naturally in the sand beneath an infested turnip. The damaged plant was removed just before the start of the test.
- *Artificially buried hosts.* The host patch consisted of 10 *D. radicum* pupae artificially buried in clean sand.

EXPERIMENTS

Distribution and location of eggs

The test arena was divided into a 7×7 grid using 49 square plastic boxes (6×6 cm) which were filled with moist sand until the boxes were slightly buried, so that the floor of the test arena was one continuous surface. One *A. bilineata* female was introduced for 48 h in this test arena and then beetle eggs were collected by flotation and counted (each square being examined for eggs separately). To determine the influence of the foraging environment on the distribution and location of eggs, three treatments were compared: (1) artificially buried hosts only; (2) undamaged plant with *D. radicum* eggs in the central square and artificially buried hosts in another square; and (3) sand only.

The group of artificially buried pupae was placed into a square, selected at random (excluding the squares forming the sides of the arena, as well as the central square). The test was replicated 10 times in each condition.

The distribution of eggs in the test arena was analysed using the I_8 index of dispersion (Morisita 1962). The effect of the treatment on the total number of eggs laid was determined through an ANOVA, using GLIM 3.77 (Crawley 1993).

Oviposition site selection

The oviposition site preference of *A. bilineata* females was evaluated in dual choice experiments by introducing one female for 48 h into an arena with two oviposition sites.

In the first set of experiments, to determine which cues coming from the host plant and/or from the different host stages play a role in oviposition site selection, females were given the choice between a standard oviposition site consisting of one undamaged plant surrounded with *D. radicum* eggs and one of the five following sites: (1) undamaged plant; (2) damaged plant with unparasitized host pupae; (3) naturally buried hosts pupae; (4) damaged plant; and (5) crushed damaged plant.

In the second set of experiments, to rank the different attractive cues tested in the first set, females were offered one of the following dual choices: (1) damaged plant vs. crushed damaged plant; (2) damaged plant vs. damaged plant with unparasitized host pupae; and (3) damaged plant with unparasitized host pupae vs. damaged plant with parasitized host pupae.

Oviposition site preference was analysed using chi-square tests. The effect of the site types on clutch size was evaluated with ANOVA using GLIM 3.77 (Crawley 1993).

Results

DISTRIBUTION AND LOCATION OF EGGS

The presence of a host plant or host insects affected greatly the number of eggs laid by the female beetles ($F_{2,27} = 416.5$; $P < 0.001$). Females laid more eggs when a host plant, eggs or pupae of *D. radicum* were present. The distribution of eggs was aggregated ($I_8 > 1$, F -test; $P < 0.01$). Eggs were laid in those squares that contained fly eggs or pupae, or in the immediately adjacent squares (Table 1). When given the choice between the half turnip inoculated with *D. radicum* eggs and an artificial patch of buried fly pupae, females laid most eggs near the plant (Table 1).

OVIPOSITION SITE SELECTION

First set of experiments

When females had the choice between a standard oviposition site consisting of one undamaged plant inoculated with *D. radicum* eggs and the following.

1. One *undamaged plant*; females showed a strong preference for the standard oviposition site ($\chi^2 = 12.70$, d.f. = 1, $P < 0.001$) (Fig. 1).
2. One *damaged plant with unparasitized host pupae*; females showed a strong preference for the damaged plant with the host pupae ($\chi^2 = 131.28$, d.f. = 1, $P < 0.001$) (Fig. 1).
3. *Naturally buried hosts*; the females did not show any preference ($\chi^2 = 0.47$, d.f. = 1, $P > 0.05$) (Fig. 1).
4. One *damaged plant*; the females preferred the damaged plant ($\chi^2 = 8.89$, d.f. = 1, $P < 0.001$) (Fig. 1).
5. One *crushed damaged plant*; the females preferred the crushed damaged plant ($\chi^2 = 14.10$, d.f. = 1, $P < 0.001$) (Fig. 1).

Hence, the type of oviposition site present in the test arena affected greatly the number of eggs laid by *A. bilineata* females ($F_{5,91} = 9.72$, $P < 0.001$) (Fig. 1).

Second set of experiments

1. One *damaged plant vs. one crushed damaged plant*; the females preferred to lay on the damaged plant ($\chi^2 = 59.59$, d.f. = 1, $P < 0.001$) (Fig. 2).

Table 1. Mean fecundity (\pm SEM), location and distribution of *A. bilineata* female eggs in test arenas containing clean sand (control) or artificially buried hosts or one undamaged plant with *D. radicum* eggs and artificially buried hosts. Equal letters indicate no significant difference between means ($P > 0.05$). I_8 is the dispersion index. F -test indicates the significant deviance of the I_8 index from 1 for $P < 0.05$

	Control	Artificially buried hosts	Artificially buried hosts/plant/eggs
n	10	10	10
Mean fecundity (\pm SE)	0.6 \pm 0.95	7.1 \pm 3.98	9.9 \pm 3.79
Duncan (multiple-range test)	B	A	A
% of eggs laid			
On patch of pupae	–	72.8	3.1
On plant	–	–	68.4
Adjacent areas to patch of pupae	–	8.5	9.1
Adjacent areas to plant	–	–	10.1
Other areas	100	19.7	16.1
I_8	136.11	52.64	30
F -test	**	**	**
	($F = 3.21$; $P < 0.01$)	($F = 8.39$; $P < 0.01$)	($F = 6.81$; $P < 0.01$)
Distribution	aggregated	aggregated	aggregated

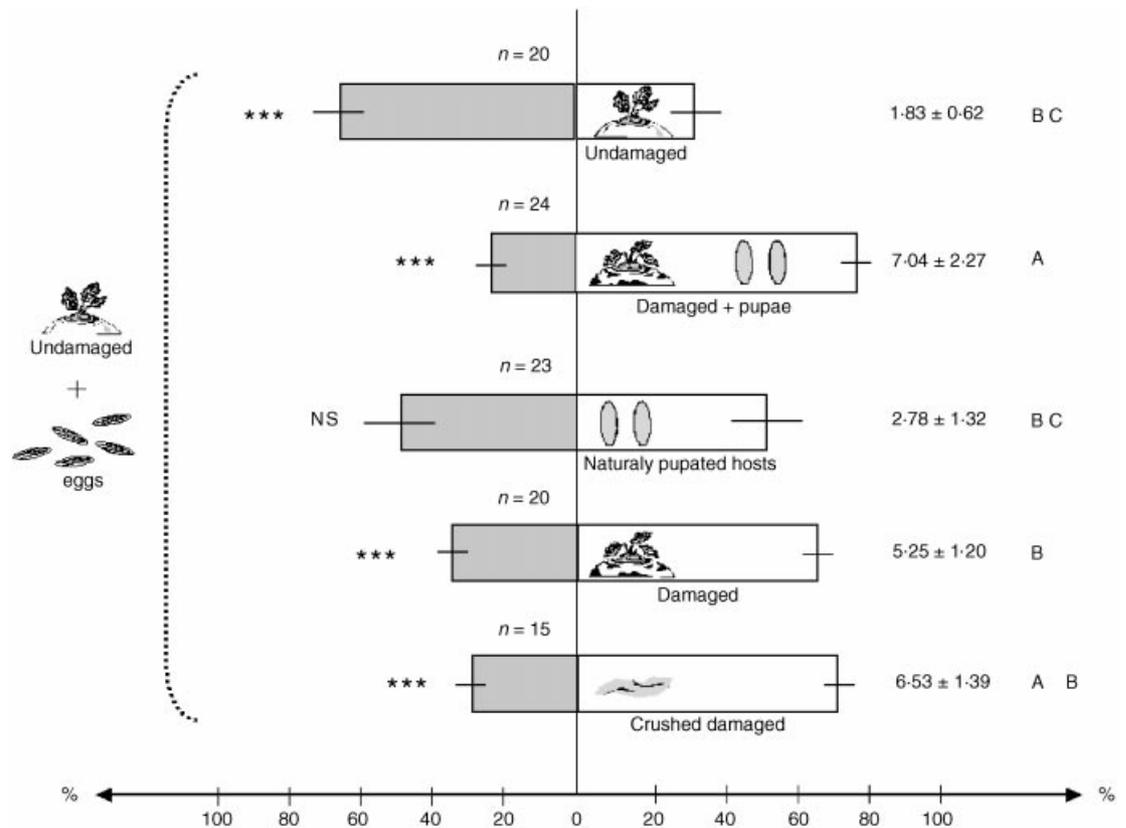


Fig. 1. Proportions ($\% \pm$ SE) and mean (\pm SEM) numbers of eggs deposited on each site by *A. bilineata* females in dual choice experiments between a control site (undamaged plant with *D. radicum* eggs) and different types of sites. Asterisks indicates the level of significance of χ^2 tests (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$) and n indicate the number of replicates for each dual choice. Equal letters indicate no significant differences among means of eggs deposited on non-control sites (Duncan test).

2. One damaged plant vs. one damaged plant with unparasitized host pupae; the females preferred the damaged plant with the host pupae ($\chi^2 = 55.23$, d.f. = 1, $P < 0.001$) (Fig. 2).

3. One damaged plant with unparasitized host pupae vs. one damaged plant with parasitized host pupae; the females preferred the site that contained the unparasitized pupae ($\chi^2 = 10.8$, d.f. = 1, $P < 0.01$) (Fig. 2).

Discussion

In coleopteran parasitoids such as *A. bilineata*, host location and selection was considered to be performed exclusively by first instar larvae (Eggleton 1993; Godfray 1994). Consequently, the females were supposed to have a weaker influence on their reproductive success than females of hymenopteran parasitoids, which are

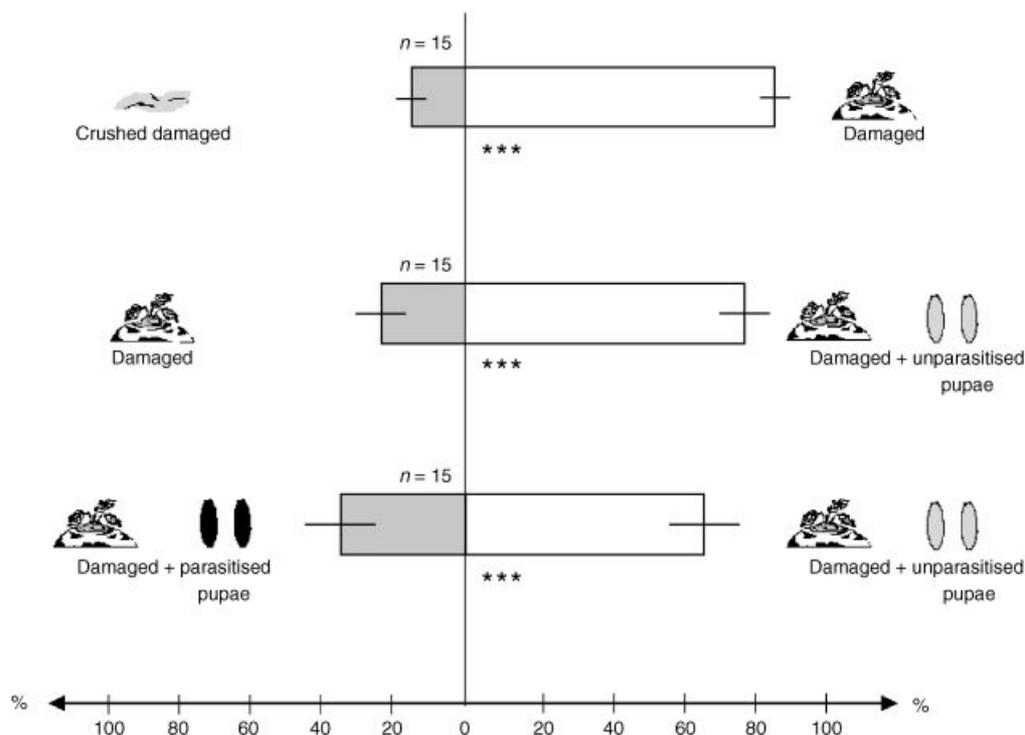


Fig. 2. Proportions (% \pm SE) of eggs laid on each site and oviposition site preference of *A. bilineata* females in dual choice experiments. Asterisks indicate the level of significance of χ^2 tests (* P < 0.05; ** P < 0.01; *** P < 0.001) and n indicates the number of replicates for each dual choice.

directly involved in host selection. However, in *A. bilineata*, oviposition site selection by females can strongly influence subsequent larval survival, as parasitoid larvae have only a short life expectancy (Fournet 1996) and become less and less selective about host quality as hours go by (Royer *et al.* 1999).

In the present study, we investigated how the information available in their foraging environment affected where the females laid their eggs.

Our first experiments showed that when no host or host plant material was available in the test arena, the females laid only a few eggs. However, once host pupae were introduced with or without undamaged plant tissues, females laid significantly more eggs. Hence, such results suggest that cues associated with the host and the host plant stimulate the oviposition of *A. bilineata* females. Concerning the distribution of eggs, when only buried pupae were available, the females laid their eggs on or close to the patch of pupae. Such behaviour should reduce host searching-time for the larvae and thus enhance their probabilities to find a suitable host pupa. However, when an undamaged turnip was also present in the test arena, females laid most of their eggs on the undamaged plant, and only a few near the patch of pupae. These results were unexpected. We hypothesized that most females would lay their eggs near host pupae, even in the presence of a host plant, as pupae are the only host stage that can be parasitized by *A. bilineata* larvae.

This surprising egg distribution could be explained if most females had difficulty finding the pupae artificially buried in clean sand when a plant was placed in

the test arena. Since pupae were buried artificially in the sand, the cues associated with the host pupae may have not been sufficiently detectable in our experiment. The females probably oviposited near the undamaged plant because it was easy to find and, if more precise information could not be detected rapidly, represented the area where host pupae would normally be found. These first results question which precise cues stimulated females to make their oviposition decisions. Hence, we investigated egg distribution and clutch size from females given a choice between a half turnip surrounded with *D. radicum* eggs (standard site), and one of several other sites.

Aleochara bilineata females laid their eggs on the standard site when the other half of the turnip was undamaged by *D. radicum* larvae and did not bear *D. radicum* eggs. In all other cases, females displayed a strong preference for damaged plants, crushed or not, associated or not with *D. radicum* pupae. These results suggest that cues associated with all the *D. radicum* immature stages tested or resulting from their activity were attractive for females. In the absence of host pupae, females might have used cues associated with *D. radicum* eggs, larvae or larval frass as indicators of areas where suitable host stages could be present. Such behaviour occurs in some hymenopteran species which use highly detectable information from a host stage different from the one under attack when the different host stages frequently co-occur in the field (Wiskerke, Dicke & Vet 1993). Previous olfactometer tests also showed that *D. radicum* frass was an important cue for *A. bilineata* females (Royer & Boivin 1999).

To determine the relative contribution of cues coming from damaged plants and from host pupae to the selection of oviposition sites, both sites were tested in separate dual choices against the standard site. Females showed no oviposition site preference when they had access to naturally buried hosts only, while they still exhibited a strong preference for the damaged plant. This confirms that although females may be able to perceive specific cues associated with the pupae, pupal cues may be more difficult to detect than plant cues. Also, the suppression of the plant shape by crushing the damaged root did not affect females' preference, suggesting that the use of visual cues was probably not essential.

The number of eggs laid differed significantly among the treatments. Females laid more eggs on sites consisting of damaged plants, and the highest average number of eggs on the site where the damaged plant was associated with host pupae. In gregarious hymenopteran parasitoids, females adjust the size and sex ratio of their clutch to the quality of the host. Large hosts provide more food for the immature stages of the parasitoids and thus ensure that numerous larvae will develop successfully. As a result, ovipositing larger clutches in high quality hosts (i.e. usually large) maximizes female fitness (Salt 1961; Le Masurier 1987; Godfray 1994). Thus, we propose that, in the case of *Aleochara* females, the oviposition site consisting of the host microhabitat (the turnip root) could be considered as the equivalent of a single host for gregarious hymenopteran parasitoids. Hence, the quality of this oviposition site could be measured as the probability that a host-seeking larva, hatching at this site, would find a suitable pupa quickly. Site quality would then increase with the presence of the successive host stages, sites where the adult female could detect the presence of numerous fly pupae being of the highest quality.

As our results showed that damaged plants alone, crushed damaged plants and damaged plants with host pupae were all suitable oviposition sites for *A. bilineata* females, we tried to rank the different stimuli used by females to evaluate the quality of oviposition sites.

Aleochara females displayed a strong preference for damaged plants with host pupae compared to damaged plants without pupae. This result confirms that females are able to detect the presence of the pupal stage, by using specific cues associated with the host pupa itself. Also, females exhibited a strong preference for the damaged plant when tested against the crushed damaged one, suggesting that although not essential, visual cues may also play a role in oviposition site selection.

Moreover, our results show that *Aleochara* females are able to perceive very specific information about the status of the host pupae. Indeed, females oviposited preferentially on damaged plants with unparasitized host pupae rather than on damaged plants with parasitized host pupae, which indicates that *Aleochara* females are able to evaluate the parasitization status of

available host pupae. Although host discrimination is very common in hymenopteran species (van Alphen & Visser 1990) this is the first time, to our knowledge, that host discrimination is demonstrated in females of coleopteran parasitoids that oviposit away from their hosts. However, the signals used by *Aleochara* females to discriminate between sites with unparasitized and parasitized pupae remain unknown. Females could perceive the presence of competitive larvae in the potential host pupae, traces of these larvae in the environment or signs of parasitization of the potential host pupae, such as a penetration hole in the puparium or wounding of the pupae by the ectophagous larva. Also, discrimination between sites with unparasitized and parasitized pupae may result from the detection of marks present either on the host pupae or in the entire patch as it has been shown in some hymenopteran parasitoids (van Alphen & Visser 1990; van Dijken, van Stratum & van Alphen 1992; Bernstein & Driessen 1996).

As mentioned previously, Hymenopteran parasitoids and coleopteran parasitoids such as *A. bilineata* exhibit quite different life history traits, particularly in terms of host location and selection. However, our study shows that in response to the quality of oviposition sites, *A. bilineata* females display the same adaptive oviposition behaviours as hymenopteran parasitoids in response to the quality of hosts. *Aleochara bilineata* females adapt their oviposition decisions and their clutch size to the presence of the host, its development stage and parasitization status. By selecting sites where pupae are present, and by further discriminating between already exploited sites and unexploited ones, *A. bilineata* females increase the probability that their progeny will find hosts at the right development stage for parasitization, and that these hosts are of high quality in terms of parasitization status. Such a behaviour may strongly improve both the parasitization and survival rates achieved by host-seeking larvae, and thereby enhance female fitness.

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