

OVOPOSITION BEHAVIOUR OF *EPHEDRUS CERASICOLA*
[HYM. : APHIDIIDAE] PARASITIZING DIFFERENT INSTARS
OF ITS APHID HOST

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The parasitoid *Ephedrus cerasicola* Stary oviposited in all 4 nymphal instars and in newly moulted adults of *Myzus persicae* (Sulzer). The different host categories were offered with no choice. The duration of an oviposition increased with the age of nymphs, being about 13, 18, 21, 22, and 17 s from 1st instars to adults, respectively. Observations of number of stabbing attacks prior to oviposition, percent of the encounters not resulting in oviposition, time from first encounter to oviposition, handling time and aphid defensive behaviour also indicated that 1st instar *M. persicae* are most easily parasitized.

The behaviour of *E. cerasicola* in encounters with unparasitized and parasitized hosts, suggested that the parasitoid could discriminate. In encounters with parasitized 1st to 4th instar aphids, *E. cerasicola* used only the antennae in 80 % of the encounters that resulted in discrimination.

KEY-WORDS : *Ephedrus cerasicola*, *Aphidiidae*, *Myzus persicae*, oviposition, host instar, discrimination.

In contrast to most other *Aphidiidae*, oviposition in the genus *Ephedrus* lasts for several seconds (Stary, 1962 ; Dureseau *et al.*, 1972). Therefore direct observations of oviposition can easily be carried out in species of *Ephedrus*.

Detailed information on oviposition behaviour in *Ephedrus* has not been reported. The present study examines this behaviour of *Ephedrus cerasicola* Stary, a species that parasitizes all nymphal instars and adult apterae of *Myzus persicae* Sulzer. Hofsvang & Hågvar (1975, 1978, 1983a,b) have earlier studied some aspects of the biology of *E. cerasicola*.

MATERIALS AND METHODS

E. cerasicola was reared on *M. persicae* feeding on swedes (*Brassica napus rapifera* Metzger). Female parasitoids which were observed to oviposit in the aphid colony, were chosen for the experiments, and hence all the parasitoids were considered to be experienced. Females of various ages were used.

Adult *M. persicae* were taken from colonies on swedes or paprika (*Capsicum annum* L.) and reared at 21 ± 1°C, 16 h light. The aphids were checked each day and offsprings that were up to 1 day old, were isolated in a Petri-dish at 21 ± 1°C and 16 h light on fresh

paprika-leaves floating on water or stored on foam rubber soaked with water. The aphid instars were determined on the basis of cast skins. In 4th instar and adults only apteriform and apterae, respectively, were used.

In the oviposition experiment, a single *E. cerasicola* female was placed in a Petri-dish with a diameter of 5 cm containing a single *M. persicae* on a small piece of paprika leaf. From the 1st encounter between the parasitoid and the aphid and onwards, the time for and duration of each new encounter was recorded. Duration of oviposition and handling time were measured in seconds. Handling time is defined as the duration of that encounter ending in oviposition, including the oviposition period. The behaviour of the parasitoid female (antennal contact, stabbing attack, oviposition etc.) was observed. The observations usually were continued for 5 mn after the 1st encounter, but in some instances they were continued for longer if the oviposition was delayed. In some of the experiments where the aphids were parasitized in 1st and 2nd instar, a few aphids belonging to the same instar were placed together in the Petri-dish, but then only the duration of the oviposition period was measured.

TABLE 1

Per cent M. persicae belonging to different instars showing defensive behaviour (jerking with abdomen/walking away) when encountered by a female E. cerasicola (n = number of aphids encountered)

Instar	Per cent with defensive behaviour	n
1	13	15
2	18	33
3	29	88
4	26	161
Adult	80	20

Nymphal instars : $\chi^2 = 2.8$, $p > 0.3$

Nymphal instars combined compared with adults : $\chi^2 = 26.8$, $p < 0.001$

After parasitization, the aphids were stored in a Petri-dish at $21 \pm 1^\circ\text{C}$ and 16 h light on paprika-leaves. The leaves were floated on water (aphids parasitized in 1st and 2nd instar and as adults) or stored on foam rubber soaked with water (aphids parasitized in 3rd and 4th instar, and some in 1st and 2nd instar ($n = 14$ and 33 , respectively)). The aphids were shown to be parasitized either by dissection or by letting the aphids develop into a mummy. However, *E. cerasicola* seemed to have great difficulties in parasitizing adult *M. persicae*. To increase the number of adult aphids, 14 adults were therefore included that received the typical long sting, but which did not contain a parasitoid larva by later dissections.

Data on superparasitization refer to observations of ovipositions lasting for at least 9 s.

The effect of aphid instar on parasitoid behaviour was tested by one way analysis of variance, followed by Student t-test, sometimes modified according to Welch (1947) when the variances of 2 series differed greatly. χ^2 test for homogeneity was used to compare percentages. Level of significance : 5 %.

RESULTS

In the experiments in which a parasitoid female searched for a single aphid host on a leaf fragment in a Petri-dish, the general oviposition behaviour was as follows : *E. cerasicola* walked at random, drumming with the antennae on the surface in front of her. Unless

contact was made, the aphid was never attacked, even if the antennae of the parasitoid came to within 1-2 mm from the aphid. An encounter with an aphid host was initiated only by antennal contact, and was followed directly by oviposition or by several stabbing attacks prior to oviposition. A stabbing attack lasted for less than 1 second, an oviposition for several seconds (table 2). Immediately after the oviposition was performed, the parasitoid left the aphid.

TABLE 2

No. of stabbing attacks prior to oviposition, oviposition period and handling time in seconds for different instars of M. persicae parasitized by E. cerasicola. Means followed by the same letter are not significantly different (t - test)

n = no. of aphids

Aphid instar	Aphid size (mm)	n	No. of stabbing attacks	n	Oviposition period (s.)	n	Handling time (s.)	n
	(x ± S.D.)		(x ± S.D.)		(x ± S.D.)		(x ± S.D.)	
1	0.7 ± 0.1	14	0.6 ± 0.9a	14	13.6 ± 3.8a	59	22.6 ± 10.1a	14
2	0.9 ± 0.1	104	1.4 ± 2.2ab	33	17.6 ± 5.4b	126	44.0 ± 30.2bc	33
3	1.1 ± 0.2	82	1.1 ± 2.2a	82	20.7 ± 9.2cd	82	40.3 ± 27.8bc	82
4	1.4 ± 0.2	110	2.4 ± 3.3b	110	22.4 ± 15.3c	110	45.9 ± 47.3b	110
Adult*	1.5 ± 0.1	23	12.2 ± 13.8c	23	17.4 ± 5.7bd	23	74.6 ± 82.8c	23

* Only 9 aphids were positively shown to be parasitized.

The most frequent defensive response of aphids that was observed during encounters with a parasitoid, was a sudden jerking with its abdomen. In other cases, the aphid walked away, sometimes with the ovipositing parasitoid in tow. Per cent *M. persicae* in the different instars showing a defensive behaviour when attacked by a female parasitoid, are given in table 1. There is a significant difference between nymphal instars combined and adult *M. persicae* in defending themselves, the defence being much stronger in the adults. It was also observed that several aphids in a colony simultaneously started to jerk their bodies in the same characteristic manner as soon as one of them was attacked by a female parasitoid.

If the oviposition process of *E. cerasicola* was disturbed during the 1st encounter, one or several new encounters were established before oviposition was performed. Stabbing attacks could be observed during these encounters and even in new encounters after oviposition. The number of stabbing attacks prior to oviposition, the duration in seconds of oviposition and handling time, are given in table 2 for each instar of *M. persicae*. The size of the aphids in the different instars is also shown. Aphid instar influenced the number of stabbing attacks ($F = 25.42$, $p = 0.0001$), which was significantly higher with adult hosts than nymphs. Oviposition period was also influenced by host instar ($F = 9.30$, $p = 0.0001$) and increased up to 4th instar. No difference was found in oviposition period in adult aphids between those that were positively shown to be parasitized and those that were not (t -test, $p = 0.4$). The minimum time for oviposition in different instars of *M. persicae* was 9 s. In addition, the following attacks were noted where no parasitization could be demonstrated: 4 s (1st instar, 2 observations), 8 s (4th instar), 7, 8 and 9 s (3 observations of adult aphids). No relationship between the duration of oviposition and the age of the parasitoid female could be shown. Handling time was significantly influenced by aphid instar ($F = 3.83$, $p = 0.0049$) and was shorter in 1st instar aphids.

In encounters with *M. persicae*, *E. cerasicola* showed a tendency towards increasing difficulties in parasitizing the larger hosts (table 3).

Figure 1 demonstrates discrimination ability, illustrated by the percentage of encounters between *E. cerasicola* and unparasitized and parasitized *M. persicae*, not resulting in oviposition. The differences between the 2 columns at each aphid stage are attributed to the ability of *E. cerasicola* to discriminate. All differences were significant (χ^2 test). The discrimination seems to be mainly independent of aphid instar, with the exception of the adult stage where the material is scarce because relatively few aphids became parasitized. Those females not ovipositing in already parasitized aphids, left the aphids after antennal contact only, or after antennal contact followed by stabbing attacks. Percentage of parasitized aphids rejected by *E. cerasicola* only after antennal contact was about 80 in each nymphal instar (fig. 1). How discrimination is achieved with adult hosts is uncertain due to few replicates, but it seems that stabbing attacks are more common as a part of discrimination.

TABLE 3

Behaviour of E. cerasicola in encounters with M. persicae prior to oviposition

n = no. of encounters.		N = no. of aphids				
Aphid instar	Per cent encounters not resulting in oviposition	n	Per cent encounters prior to oviposition (including oviposition encounter) having stabbing attacks	n	Average time (sec.) from 1st encounter to start of oviposition (superparasitized aphids omitted)	N
					(x ± S.E.)	
1	9.5	21	23.8 a	21	9.9 ± 2.7 a	19
2	15.0	40	50.0 b	40	48.0 ± 8.1 b	30
3	6.4	125	28.8 a	125	23.2 ± 3.0 a	93
4	27.0	159	47.8 b	159	58.0 ± 10.3 b	105
Adult*	65.2	66	77.3 c	66	244.9 ± 101.4 b	16
Values followed by the same letter are not significantly different (χ^2 test)					F = 12.9, p = 0.0001 Means followed by the same letter are not significantly different (t-test)	

* Only 9 aphids were positively shown to be parasitized.

DISCUSSION

Most female *Aphidiidae* search for aphid hosts with the antennae. The host is detected by antennal contact, followed by stabbing attacks and/or oviposition, as described for *E. cerasicola* in the present study (T'Hart *et al.*, 1978; Dransfield, 1979; Gardner *et al.*, 1984).

The duration of oviposition varies between different genera within *Aphidiidae*. Short oviposition lasting for about 1 or 2 s is recorded in *Aphidius* (T'Hart *et al.*, 1978; Dransfield, 1979; Mackauer, 1983; Shirota *et al.*, 1983). In parasitoids with a short oviposition act, e.g. *Aphidius*, it is impossible to know whether an oviposition or only probing has taken place. In *Aphidius rhopalosiphi* (DeStefani-Perez) approximately only 45 % of the stabbing attacks resulted in oviposition (Gardner *et al.*, 1984) and correspondingly only 20.1 % in *Aphidius matricariae* Haliday (T'Hart *et al.*, 1978). In *E. cerasicola* short stabbing attacks are easily distinguished from ovipositions.

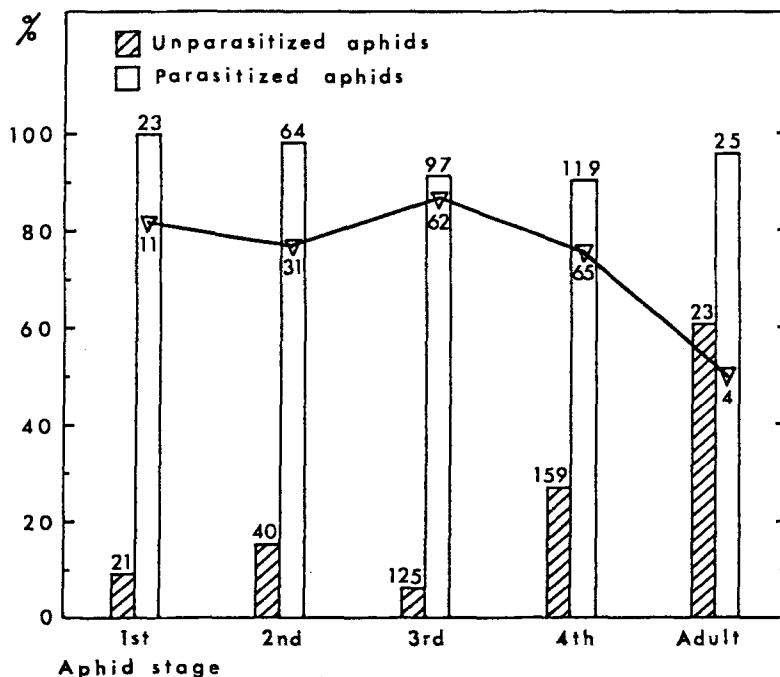


Fig. 1. Percentage encounters between *E. cerasicola* and different instars of unparasitized and parasitized *M. persicae*, not resulting in oviposition. No. of encounters is given above each column. Triangles: percentage of the discrimination encounters where only antennae were used. No. of discriminated aphids is given beneath each triangle.

No detailed information of different factors influencing the duration of oviposition is known from literature concerning *Ephedrus*. The present results show that *E. cerasicola* has a long oviposition act and needs at least 9 s to deposit an egg. The length of oviposition period increases from 1st to 4th instar of *M. persicae*, probably reflecting increasing difficulties in depositing an egg into the aphid. In adult aphids the oviposition period is lower than in 4th instar, probably due to defensive behaviour in most adults, also illustrated by the long handling time. The same tendency of increasing oviposition period with aphid age is partly shown in *A. rhopalosiphi* (expressed as "handling time" – **Shirota et al.**, 1983).

Large *M. persicae*, especially adults, have a strong defensive behaviour when attacked by *E. cerasicola*, which makes them difficult and time consuming to parasitize. The jerking behaviour of *M. persicae* is similar to that of *Metopolophium dirhodum* (Walker) when parasitized by *A. rhopalosiphi* (**Gardner et al.**, 1984). *M. persicae* is also observed to defend itself by walking away from the ovipositing parasitoid. Defensive behaviour in aphids attacked by *Aphidiidae* such as knocking away the parasitoid with legs or antennae, shaking or jerking the body, walking off or falling from the plant, have been observed in many aphid species (**Shalaby & Rabasse**, 1979; **Ankersmit**, 1982; **Singh & Sinha**, 1982; **Shirota et al.**, 1983; **Gardner et al.**, 1984; **Liu et al.**, 1984). When different aphid instars were investigated, the defence mechanisms showed to be stronger in the last nymphal instar and in adult aphids (**Shalaby & Rabasse**, 1979; **Ankersmit**, 1982; **Singh & Sinha**, 1982; **Shirota et al.**, 1983; **Liu et al.**, 1984).

Based on the present experiments in which 1 female *E. cerasicola* was allowed to parasitize a single *M. persicae*, it seems that *E. cerasicola* most easily oviposits in 1st instar aphids. Successful oviposition in large aphids seemed to be limited in *E. cerasicola* due to the combination of defensive aphids and long duration of the oviposition act. In contrast, several studies of *Aphidiidae* showed a tendency that the parasitoids especially attacked aphids in the 2nd or 3rd instars (Singh & Sinha, 1982 ; Shirota *et al.*, 1983 ; Cloutier *et al.*, 1984 ; Liu *et al.*, 1984).

Solhaug (1985) found that *E. cerasicola* preferred small aphid hosts when given a choice between 2 different size categories of *M. persicae* : small and medium nymphs, small nymphs and adults or medium nymphs and adults. In all combinations and replicates the percentage of encounters resulting in oviposition was always significantly higher for the youngest aphids available. In 1 replicate 80.3 % of encounters with small nymphs and only 6.2 % of encounters with adult aphids resulted in oviposition.

Hofsvang & Hågvar (1983) concluded from indirect evidence that *E. cerasicola* seems to discriminate between unparasitized and parasitized *M. persicae*. The behaviour of the parasitoid in encounters with unparasitized and parasitized aphids, also supports that *E. cerasicola* have this ability (fig. 1). Also when given a choice between unparasitized and parasitized *M. persicae*, significantly more unparasitized aphids were parasitized by *E. cerasicola* during the random encounters (Solhaug, 1985). In about 60 % of the encounters with unparasitized aphids, and only in about 10 % of the encounters with parasitized aphids, did oviposition take place. In *Aphidiidae* the ability to discriminate has been demonstrated for several species (T'Hart *et al.*, 1978 ; Chow & Mackauer, 1984 ; Cloutier *et al.*, 1984). However, recently, Gardner *et al.* (1984) positively have shown that *A. rhopalosiphii* did not discriminate between unparasitized and parasitized *M. dirhodum*. At least in the period just after the 1st parasitization (5-10 mn.), *E. cerasicola* usually discriminated only by means of the antennae. This indicates that such parasitized hosts are marked externally.

RÉSUMÉ

Comportement de ponte d'*Ephedrus cerasicola* [Hym. : *Aphidiidae*] dans différents stades de son hôte

Le parasitoïde *Ephedrus cerasicola* STARÝ pond dans les 4 stades larvaires et le stade adulte des virginipares aptères de *Myzus persicae* (SULZER). Les différents types d'hôtes sont présentés séparément. La durée d'oviposition augmente avec le stade, soit : 13, 18, 21, 22 et 17s dans les stades successifs. L'observation du nombre de piqûres, le pourcentage de rencontres sans oviposition, le temps de ponte et le comportement défensif des aphides traduisent la facilité avec laquelle les *M. persicae* du 1^e stade sont parasités.

Le comportement d'*E. cerasicola* au cours de ses rencontres avec des hôtes parasités ou non, indique que le parasitoïde est capable de discriminer. Au cours de ses rencontres avec des aphides du 1^e au 4^e stade déjà parasités, *E. cerasicola* n'a employé que ses antennes dans 80 % des cas où il y avait discrimination.

Received : 18 July 1985 ; Accepted : 28 November 1985.

REFERENCES

- Ankersmit, G. W. - 1982. Aphidiids as parasites of the cereal aphids *Sitobion avenae* and *Metopolophium dirhodum*. In : Aphid Antagonists (R. Cavalloro ed.). - A. A. Balkema, Rotterdam, 42-49.
- Chow, F.J. & Mackauer, M. - 1984. Inter- and intraspecific larval competition in *Aphidius smithi* and *Praon pinguicolum* [Hymenoptera : *Aphidiidae*]. - *Can. Entomol.*, 116, 1097-1107.

- Cloutier, C., Dohse, L.A. & Bauduin, F. – 1984. Host discrimination in the aphid parasitoid *Aphidius nigripes*. – *Can. J. Zool.*, 62, 1367-1372.
- Dransfield, R.D. – 1979. Aspects of host – parasitoid interactions of two aphid parasitoids, *Aphidius urticae* (Haliday) and *Aphidius uzbekistanicus* (Luzhetski) [Hymenoptera, Aphidiidae]. – *Ecol. Entomol.*, 4, 307-316.
- Dureseau, L., Rivet, E. & Drea, J.J. – 1972. *Ephedrus plagiator*, a parasite of the greenbug in France. – *J. Econ. Entomol.*, 65, 604-605.
- Gardner, S.M., Ward, S.A. & Dixon, A.F.G. – 1984. Limitation of superparasitism by *Aphidius rhopalosiphi*: a consequence of aphid defensive behaviour. – *Ecol. Entomol.*, 9, 149-155.
- T'Hart, J., De Jonge, J., Colle, C., Dicke, M., Van Lenteren, J.C. & Ramakers, P. – 1978. Host selection, host discrimination and functional response of *Aphidius matricariae* Haliday [Hymenoptera : Braconidae], a parasite of the green peach aphid, *Myzus persicae* (Sulz.). – *Med. Fac. Landbouww. Rijksuniv. Gent.*, 43, 441-453.
- Hofsvang, T. & Hågvar, E.B. – 1975. Developmental rate, longevity, fecundity, and oviposition period of *Ephedrus cerasicola* Starý [Hym. : Aphidiidae] parasitizing *Myzus persicae* Sulz. [Hom. : Aphididae] on paprika. – *Norw. J. Entomol.*, 22, 15-22.
- Hofsvang, T. & Hågvar, E.B. – 1978. Larval morphology and development of *Aphidius colemani* Viereck and *Ephedrus cerasicola* Starý [Hym. : Aphidiidae]. – *Norw. J. Entomol.*, 25, 1-8.
- Hofsvang, T. & Hågvar, E.B. – 1983a. Functional responses to prey density of *Ephedrus cerasicola* [Hym. : Aphidiidae], an aphidiid parasitoid of *Myzus persicae* [Hom. : Aphididae]. – *Entomophaga*, 28, 317-324.
- Hofsvang, T. & Hågvar, E.B. – 1983b. Superparasitism and host discrimination by *Ephedrus cerasicola* [Hym. : Aphidiidae], an aphidiid parasitoid of *Myzus persicae* [Hom. : Aphididae]. – *Entomophaga*, 28, 379-386.
- Liu, Shu-Sheng, Morton, R. & Hughes, R.D. – 1984. Oviposition preferences of a hymenopterous parasite for certain instars of its aphid host. – *Entomol. Exp. Appl.*, 35, 249-254.
- Mackauer, M. – 1983. – Quantitative assessment of *Aphidius smithi* [Hymenoptera : Aphidiidae] : fecundity, intrinsic rate of increase, and functional response. – *Can. Entomol.*, 115, 399-415.
- Shalaby, F.F. & Rabasse, J.M. – 1979. On the biology of *Aphidius matricariae* Hal. [Hymenoptera : Aphidiidae], parasite on *Myzus persicae* (Sulz.) [Homoptera, Aphididae] – *Moshtohor, Ann. Agric. Sc.*, 11, 75-96.
- Shirota, Y., Carter, N., Rabbinge, R. & Ankersmit, G.W. – 1983. Biology of *Aphidius rhopalosiphi*, a parasitoid of cereal aphids. – *Entomol. Exp. Appl.*, 34, 27-34.
- Singh, R. & Sinha, T.B. – 1982. Bionomics of *Trioxys (Binodoxys) indicus* Subba Rao & Sharma, an aphidiid parasitoid of *Aphis craccivora* Koch. XIII. Host selection by the parasitoid. – *Z. Angew. Entomol.*, 93, 64-75.
- Solhaug, T. – 1985. Vertsstrrelsesvalg og vertsdiskriminering for *Ephedrus cerasicola* Starý [Hymenoptera : Aphidiidae], en parasitoid på ferskenbladlus (*Myzus persicae* (Sulzer)). – Unpublished cand. real. thesis, University of Oslo (in Norwegian).
- Starý, P. – 1962. Bionomics and ecology of *Ephedrus pulchellus* Stelfox, an important parasite of leaf-curling aphids in Czechoslovakia, with notes on the diapause [Hym. : Aphidiidae]. – *Entomophaga*, 7, 91-100.
- Welch, B.L. – 1947. The generalization of "Student" problem when several different population variances are involved. – *Biometrika*, 34, 28-35.