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Behavior of *Edovum puttleri* Grissell (Hym. Eulophidae) on *Leptinotarsa decemlineata* (Say) (Col. Chrysomelidae) eggs and study on their fate. (*)

I. Introduction

A wide number of studies have had to be conducted on the biology of the recently discovered oophagous parasitoid *Edovum puttleri* Grissell (Hym. Eulophidae) with a view to its use in the biocontrol of *Leptinotarsa decemlineata* (Say) (Col. Chrysomelidae).

Edovum puttleri, which has been reared at the "Guido Grandi" Institute of Entomology since 1986 (Maini *et al.*, 1986; Maini and Nicoli, 1990) belongs to the colombian biotype imported into Italy from the United States in 1985 (Bin and Colazza, 1988). Its ability to effectively limit *Leptinotarsa* (CPB) populations in potato crops has been studied both in greenhouse and open field conditions (Pucci and Dominici, 1988; Williams, 1987; Maini *et al.*, 1990). The purpose of this study was to gain further information on the biology of this parasitoid. In particular, the study was aimed at: 1. examining the behavior of *Edovum* females on *Leptinotarsa* egg masses, which has already been described by Gardenghi *et al.* (1990) but which is studied here in greater detail; 2. evaluating the qualitative and quantitative effects of this behavior on the host eggs; 3. identifying any marking left on and/or inside the CPB egg by the female after it has parasitized or even only visited and/or punctured the egg.

II. Materials and methods

The *Edovum puttleri* females employed for this study derive from several specimens furnished by Professor Bin of the Faculty of Agriculture of the University of Perugia in 1986. The specimens were used at the "Guido Grandi" Institute of Entomology of the University of Bologna for reproduction and were reared in a climatic chamber at temperatures of 20 ± 2 °C during the night and 27 ± 2 °C during the day, a relative humidity of 80 ± 5% and a photoperiod of 16 h L : 8 h D.

Leptinotarsa decemlineata was also reared at the same Institute in order to

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obtain host eggs. Rearing was made in a fiberglass-reinforced plastic greenhouse at temperatures ranging from 17 °C during the night to 26 °C during the day in winter and from 18 °C to 32 °C in summer, and with a constant photoperiod of 16 hours light and 8 hours dark. *Solanum tuberosum* was also grown in the same greenhouse.

Observations were carried out both directly, using a stereomicroscope and behaviors duly recorded, and with a VHS videorecording system fitted to the microscope eyepiece.

The *Edovum* female was placed in a 32 mm diameter transparent box together with no more than 24-hour-old CPB eggs. The exact position of each egg in the egg mass was noted and recorded so as to be able to subsequently identify it and to determine its fate after having taken note of the activity performed on it by the *Edovum* female.

A CPB egg mass was brought into contact with each female under observation at regular intervals of 3.5 days for two consecutive hours. This time interval was chosen on the basis of previous observations as it was seen to ensure an optimum level of activity and attraction of the female towards the host eggs. The conditions at which the observations were made i.e., a single *Edovum* female acting on an egg mass of 25 CPB eggs, were fairly similar to those found in nature.

III. Results

1. - Behavioral observations

Upon being placed in a box together with a CPB egg mass, the *Edovum* female explores the environment keeping its antennae stretched out horizontally. The position of the female's antennae is the same as that encountered when the individual is frightened. This behavior was termed by us "searching".

Initially the *Edovum* female does not seem to be attracted by the host egg mass as it comes into contact with it only after having leaped around for a while inside the box. This searching behavior is, however, not exhibited once the female has visited the egg mass and acted upon it, moving away for a few minutes before returning to it. In this case it moves back heading directly and decidedly towards the eggs. Upon coming into contact with the CPB egg mass, the *Edovum* female regularly performs a number of actions in the following sequence:

1) The female moves over and around the egg mass for a few seconds keeping its antennae bent at a right angle and drumming the eggs with them. It then stops on one of the eggs and continues drumming it on various points of the surface for 20 to 30 seconds and turning around from head to tail even up to 5 or 6 times. We have termed this action "drumming".

2) The female then raises itself up on its legs bending down its abdomen until the rear tip touches the CPB egg chorion. The ovipositor, located in a ventral groove and slightly protruding from the rear tip of the abdomen, thus comes to be pointed towards the egg ("raising and ovipositor positioning") and is unsheathed ("ovipositor unsheathing") by means of a sharp back movement of the abdomen.

3) Then, with considerable effort, the female pushes the tip of the terebra against the egg, gripping the egg with its legs until, after about 1 or 2 seconds, it manages to bore the chorion ("drilling").

At this point, the female may act in one of three different manners, each of which clearly identifiable. We have termed these three patterns behaviors A, B and C.

Behavior A. Once it has bored the chorion, the female introduces its terebra by about 3/4 of its length into the egg ("ovipositor partial entering"), moving it about inside both by directly moving the organ itself and by sideway movements of its abdomen ("yolk stirring"). After about 20 to 30 seconds, the female raises itself up and withdraws the ovipositor ("removing"), which is immediately pulled back into its sheath by the appropriate ligaments.

Upon having removed the ovipositor, the female turns around in circles or moves backward, drinking the drop of egg yolk flowed out of the puncture in 2 or 3 seconds ("feeding"). Immediately afterwards, it returns to its drilling position, this time keeping its ovipositor within the sheath and tapping the egg surface with the tip of its abdomen ("tapping") all around the puncture for about 10 to 30 seconds. As shall be seen further on, the female apparently leaves an odorous mark on the egg chorion by this tapping behavior. The entire sequence of behavior A, from drilling to tapping, lasts from a minimum of 30 to a maximum of 70 seconds (fig. I).

Behavior A can be repeated several times (4 to 5 on average, and exceptionally up to 18 to 20). Moreover, the female often drills the egg again in the same position or in a position close to where it had drilled it the first time.

Behavior B. This behavior is performed by the *Edovum* female after completion of behavior A or even without the latter having been carried out. This behavior is practically that of oviposition and entails the following steps: steps 1 to 3 as previously described for behavior A are carried out first, but unlike in "A", the female pushes its ovipositor fully or almost fully into the egg ("ovipositor full entering") and remains still in this position for 1 to 3 minutes. Upon having deposited its egg, the female then withdraws its ovipositor, sometimes drinking the drop of egg yolk which flows out of the puncture. Next, it drums the egg with its antennae for a couple of seconds before moving to another egg (fig. I). The female performs behavior B either on the same egg on which it had completed behavior A one or more times (nA + B) or, after having performed behavior A on one egg, it moves to another and carries out behavior B (B alone). In both cases the female feeds on the egg yolk and it appears that without this action it is unable to bring ovogenesis to completion.

In about 56-59% of behaviors B, before changing egg the female raises itself up on its legs as in the "raising and ovipositor positioning" step, and then lowers its abdomen to touch the chorion, moving forward so as to rub the tip against the host egg. This rubbing action, which is repeated 2 to 3 times, can be safely defined as "marking" even though it does not appear to be essential for the egg to be subsequently identified as having been parasitized. As a rule, the female performs behavior B only once on the same egg and at the peak of its maturity (from between 1 to 4 weeks of imaginal life) it is capable of performing this behavior up to 12 to 16 times a day, thus parasitizing an equal number of eggs.

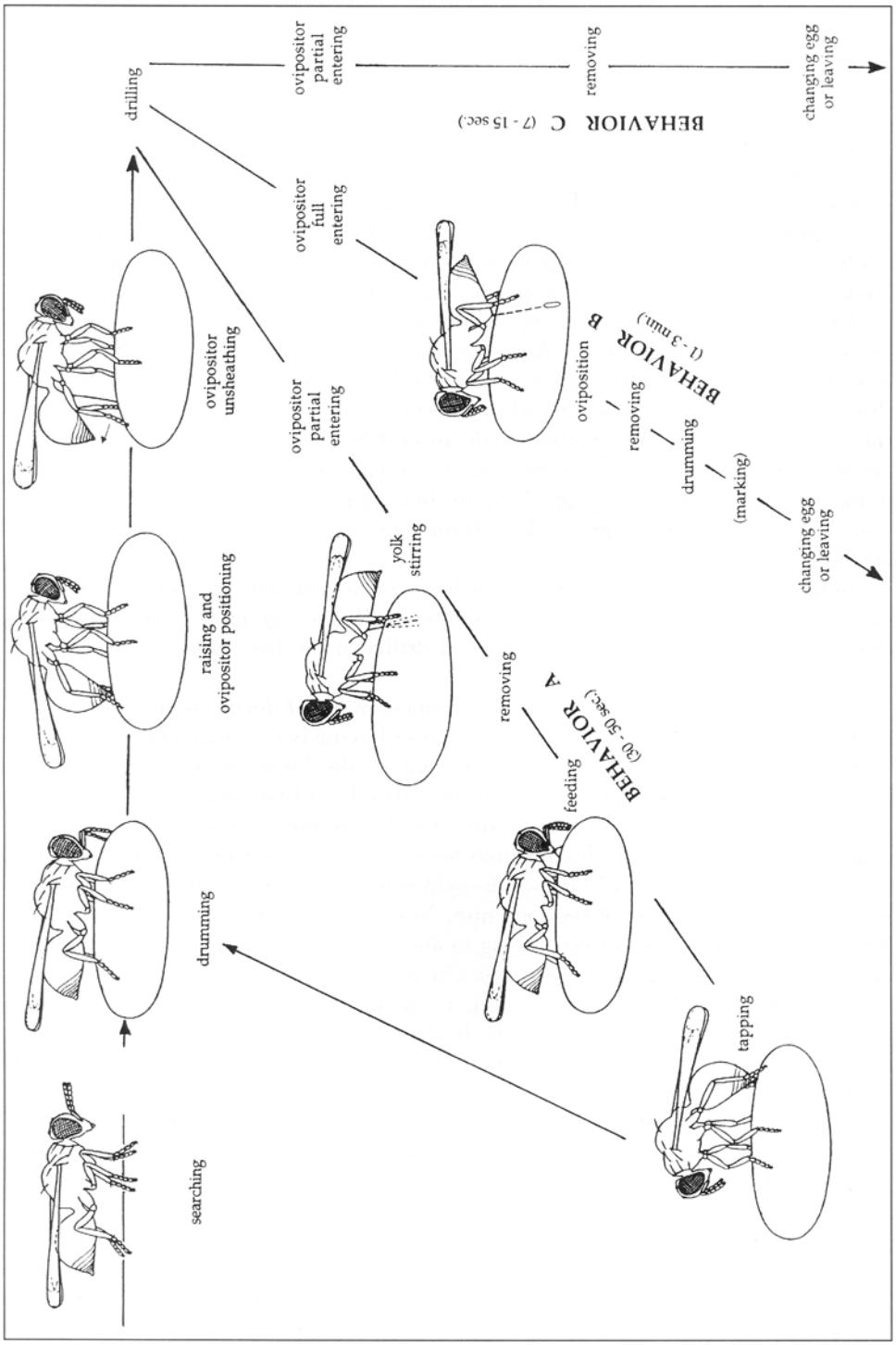

Figure I. - The three behavioral patterns A, B, and C of the *Edovum puttleri* female.

Behavior C. The Eulophidae female rapidly goes through steps 1 to 3 as described in behavior A, introducing its ovipositor by about half its length into the egg. It does not then continue on to yolk stirring or feeding, but terminates this sequence by removing its terebra from the egg. This sequence lasts on average about 11 seconds. Behavior C is performed only once on each egg, rarely twice, after which the female changes egg moving over the egg mass (fig. I).

Behavior C may be observed once the female has performed behaviors A and B many times on an egg mass and therefore after it has abundantly fed on the egg yolks and oviposited i.e., after having damaged about 20 eggs. If intact host eggs are still available, the female acts both upon these and on those which have already been subjected to behaviors A and/or B. With this behavior, it devitalizes the host eggs which are still alive or intact and often continues to oviposit if it finds eggs which have not yet been parasitized. It should however be noted that in general a few host eggs are not damaged, either because covered over by other eggs in the egg mass or because the *Edovum* female is not attracted to them. Moreover, some of the host eggs, even if subjected to behaviors A and/or C, are still capable of developing into CPB larvae.

Behavior C is carried out even when a female comes into contact with an egg mass which has already been visited and partially parasitized by another female. If, however, some intact eggs are added to the egg mass, then the second female also performs behaviors A and/or B. It should also be noted that behavior C is frequently exhibited also by very young adult females at a pre-oviposition stage, even after a few hours and up to 1 to 2 days after emergence, as well as by old females which have ceased to oviposit.

Briefly summing up, then, the following pattern emerges: during behavior A the female feeds on the host egg yolk poisoning, in a more or less substantial manner, the egg itself; during behavior B oviposition takes place and the parasitized egg is often marked; during behavior C the egg is poisoned by the female as in behavior A and, in addition, it seems that the female also probes the egg. Finally, it may be noted that the activity of a female on an egg mass at the peak of its parasitizing capacity (from a few days up to a month of age) lasts for about 2 hours, during which time the female feeds to satiation on the yolk, carries out various ovipositions and performs several C-type behaviors before leaving the egg mass.

2. - Effects of behavior A

In order to evaluate the effects of behavior A, whether single or repeated, on CPB eggs, about fifty *Edovum* females were individually observed in full activity on egg masses each comprising about 25 eggs, for a total of more than 2000 CPB eggs. It was hypothesized that during boring the *Edovum* female injects poison into the CPB egg and that, as it proceeds in its activity over the day, it may run out of poison. To verify this hypothesis, the eggs which had been subjected to behavior A were identified and subdivided according to the time of the day in which they had undergone this treatment, namely at the beginning (eggs 1 to 5), in the middle (eggs 6 to 14) and at the end of the day (eggs 15 to 25). Three stocks of eggs were thus obtained, which were also classified depending on the number of times they had undergone behavior A.

Table 1 - Effects of behavior A (including host feeding) in the course of the daily activity of the *Edovum* female on a CPB egg mass. Trend visualization.

I stock (1st - 5th egg)			II stock (6th - 14th egg)			III stock (15th - 25th egg)		
hatched CPB	aborted CPB	dead CPB eggs	hatched CPB	aborted CPB	dead CPB eggs	hatched CPB	aborted CPB	dead CPB eggs
90	50	87	63	74	132	15	54	89
39,65%	22,03%	38,32%	23,42%	27,51%	49,07%	9,49%	34,18%	56,33%

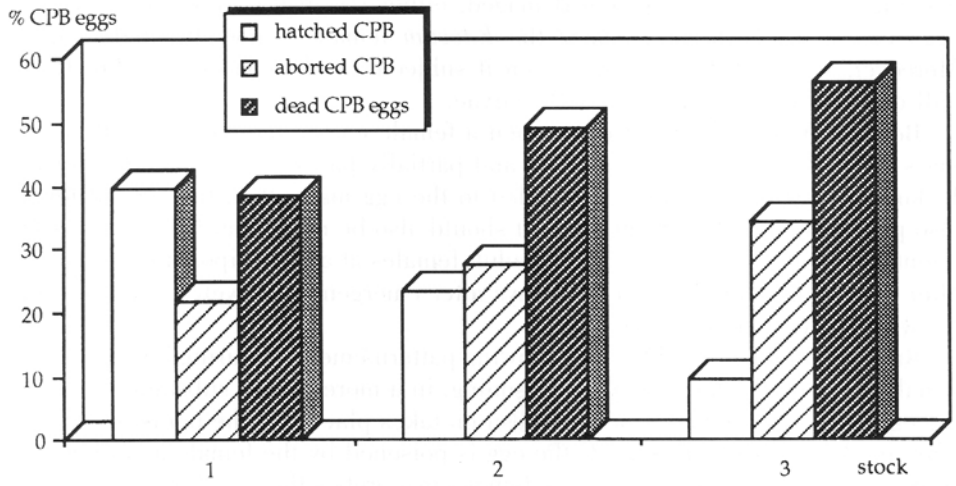

Table 1 shows the effects of behavior A on the three stocks of eggs, while table 2 shows the number of times each egg had been subjected to this behavior. As can be seen, three types of effects are possible: 1) development of the CPB larva; 2) CPB abortion; 3) collapse of the CPB egg in which the embryo had not even visibly begun to develop. CPB abortion refers to those cases in which the embryo perished after having reached a rather advanced stage of development so much so that it was clearly visible inside the egg, even if deformed or incomplete, through the chorion, also thanks to its dark spiracles.

As can be seen in table 2, the number of behaviors A (one, two or three per egg) did not seem to have any significant effect on the eggs, while the time of the day in which the egg was bored had a significant effect on its fate. In fact, hatching occurred on average in 46% of the eggs of the first stock (1st column), 25% of the second (4th column), and only 10% of the third (7th column). Table 2 also shows that the CPB eggs of the 1st stock fail to hatch after having been subjected to more than seven behaviors A (1st column), those of the 2nd stock after more than four (4th column), and those of the third after more than three (7th column).

These results would seem to suggest that as its activity on the egg mass progresses, the female injects a greater amount of or a more potent poison into the eggs. This may be due to the fact that as it bores the egg the female also feeds on the highly energetic egg yolk. CPB eggs which have been subjected to 10 or more behaviors A only very rarely develop into larvae.

Even if the majority of punctured eggs perish (aborted larvae + dead eggs), some eggs manage to survive either because they are covered over and protected by the egg mass or because they have undergone a limited number of behaviors A. Upon hatching, the surviving CPB larvae immediately start feeding on the surrounding unhatched CPB eggs, thus also destroying any *Edovum* developing in them as the latter take about one week longer to emerge than the former. This behavior is extremely important in nature as it ensures a proper host-parasitoid balance.

3. - Effects of behavior B

As can be seen in table 3, this behavior is primarily associated with oviposition as a high *Edovum* birth rate (86.04%) is observed for CPB eggs which have undergone behavior B, whether alone or preceded by one or more behaviors A. It can safely be stated that a *Leptinotarsa* egg which has undergone behavior B is doomed. In fact, after 24 to 26 hours of the *Edovum* egg having been deposited inside that of the *Leptinotarsa*, the former hatches, releasing a larva which imme-

Table 2. - Effects of behavior A in the course of the daily activity of the *Edovum* female on a CPB egg mass depending on the number of behaviors A undergone by the eggs. The dotted line indicates the number of behaviors A required for the CPB eggs not to hatch.

	I stock (1st - 5th egg)			II stock (6th - 14th egg)			III stock (15th - 25th egg)		
beh.	hatched CPB	aborted CPB	dead CPB eggs	hatched CPB	aborted CPB	dead CPB eggs	hatched CPB	aborted CPB	dead CPB eggs
1 "A"	35	20	26	35	39	60	10	33	40
	43,21%	24,69%	32,10%	26,12%	29,10%	44,78%	12,05%	39,76%	48,19%
2 "A"	18	6	15	12	16	28	4	12	22
	46,15%	15,39%	38,46%	21,43%	28,57%	50,00%	10,53%	31,58%	57,89%
3 "A"	21	9	13	10	11	15	1	4	8
	48,84%	20,93%	30,23%	27,78%	30,55%	41,67%	7,69%	30,77%	61,54%
4 "A"	7	4	1	5	3	6	0	3	5
5 "A"	4	3	7	0	2	7	0	2	6
6 "A"	4	2	8	0	0	4	0	0	2
7 "A"	1	2	1	0	2	2	0	0	1
8 "A"	0	1	3	0	1	0	0	0	0

diately begins to feed on the oocyte content of the latter, which it finishes in about 4 days.

The *Edovum* female sometimes fails to deposit its egg (5.48%) as it withdraws its ovipositor before the egg, stuck in the tip, has been completely extruded. In these cases the egg is abandoned on the chorion of the CPB egg, which always collapses. This latter finding seems to suggest that during deposition the *Edovum* female injects a powerful poison which inhibits host egg development. The long time taken for the *Edovum* female to deposit its egg and occasional failures are not surprising. In fact, from observations made by us it was seen that the lumen of the ovipositor through which the egg moves is about 16 μ wide while the egg measures 85 x 285 μ. As the ovipositor is a rigid organ the segments of which do not stretch out as the egg passes through them, the strong internal pressure required for depositing the egg considerably deforms it.

Table 3 also lists the cases of aborted *Edovum*, that is those which had perished before emergence (4.24%). The remaining aborted cases (9.72%) refer to CPB eggs which after having undergone behavior B did not exhibit any apparent development, whether of the *Edovum* or of the *Leptinotarsa*, as well as to cases of failed deposition.

As can be seen in table 3, oviposition is often preceded by behavior A, which in most cases is repeated even up to 8 times and in some cases from 18 to 20 times. In conditions similar to those found in nature i.e., one female in contact with 20 or more host eggs, *Edovum* birth-rate appears to be the same even when oviposition has been preceded by behaviors A, independently of their number. The number of behaviors A which precede behavior B depends on many factors such as the need

Table 3. - Effects of behavior B (including oviposition) alone or preceded by behaviors A. Failed behaviors B refer to those cases in which the *Edovum* egg is lost because the female withdraws its ovipositor with the egg still held in the tip. In these cases, the CPB eggs always perish.

behavior n "A" +"B"	emerged *Edovum*	aborted *Edovum*	dead CPB eggs
"B" only	176	4	3
1 "A" + "B"	72	5	3
2 "A" + "B"	42	3	3
3 "A" + "B"	50	2	2
4 "A" + "B"	45	3	2
5 "A" + "B"	33	0	1
6 "A" + "B"	19	1	2
7 "A" + "B"	15	2	3
8 "A" + "B"	8	2	0
9 "A" + "B"	9	2	1
10 "A" + "B"	4	0	0
11 "A" + "B"	3	0	0
12 "A" + "B"	6	0	1
13 "A" + "B"	2	0	0
14 "A" + "B"	1	0	1
15 "A" + "B"	2	0	2
n "A" + failed "B"	0	0	31
total	487	24	55
%	86,04%	4,24%	9,72%

to feed, which is greater at the beginning of the females daily activity and lower towards the end, when the female is satiated, the urgency to oviposit or on other factors not clearly identifiable. It should also be noted that considerable individual differences in behavior have also been reported in the observations of many females.

4. - Effects of behavior C

It was first observed that the female performs behavior C almost always only once on the same egg, before moving to another. It is very rare that while searching an egg mass, a female repeats this "exploration" on the same egg. The effects of this behavior on the CPB egg was analysed by distinguishing the behaviors performed by young females emerged from 1 to 2 days from those of over 1-week-old females. Table 4 shows the effects of this behavior, the fate of the CPB eggs being classified as CPB larva development, aborted, and collapsed. As can be seen, the more serious effects of this behavior were reported for mature females (31.92 + 47.87 = 79.79% of dead eggs) than for the younger ones (29.51 + 13.11 = 42.62% of dead eggs).

Behavior C apparently has two functions. It permits the *Edovum* female to: 1) kill some of the CPB eggs; 2) find out if the egg has already been parasitized. Observation of a female acting on an egg mass of more than 25 eggs shows that after having parasitized and damaged a certain number of eggs by feeding on them, it searches the egg mass, stinging the eggs rapidly so as to explore them (which is typical of behavior C) and further damaging them, depositing an egg in those which have not yet been parasitized. The female therefore seems to perform both these functions, while very old or very young females which are not capable of ovipositing seem to accomplish only the first function.

5. - Behavior of *Edovum* females on *Leptinotarsa* eggs at an advanced stage of development

As is known, *Edovum* females are less attracted to CPB eggs which are more than 3 days old and kept at 25 °C. Under these conditions we observed that the

Table 4. Effects of behavior C (without feeding or oviposition) classified according to whether it is performed by young or mature *Edovum* females.

	young females			mature females		
	hatched CPB	aborted CPB	dead CPB eggs	hatched CPB	aborted CPB	dead CPB eggs
1 "C"	35	17	7	18	28	44
2 "C"	0	1	1	1	2	1
total	35	18	8	19	30	45
%	57,38%	29,51%	13,11%	20,21%	31,92%	47,87%

Edovum female sometimes bores these eggs and attempts to stir the yolk with its ovipositor, encountering considerable difficulty, however, due to the consistency of the embryo tissue of the CPB, so that after a while it gives up, performing several behaviors C on the egg before abandoning it. The adverse effect of this behavior on the embryo is considerable with a mortality rate of between 20 to 30%. At the peak of its intraovular development, however, the CPB larvae which is about to hatch does not appear to be affected by the rare stings inflicted upon it. The scarce interest exhibited by *Edovum* females for 3 to 4 day-old eggs clearly limits the possibility of exploiting them for the biological control of *Leptinotarsa*.

6. - Egg marking

Our findings showed that, even when a female has at least twenty eggs available, that is, more than those it can parasitize, behavior B is only very rarely repeated on the same egg (0.75%). Except for a few errors, therefore, the "engaged" signal is released and detected with a high degree of accuracy. Rubbing of the tip of the abdomen on the host egg after oviposition, an action we have termed "marking", only occurs in about 56% to 59% of the parasitized eggs and is therefore probably not decisive in signalling that the egg has been parasitized. Moreover, marking is performed rather irregularly and varies from individual to individual. The few cases in which the B-behavior is repeated twice involved both marked and unmarked eggs, no significant differences being found between the two.

In conclusion, it would appear that the behavior of the *Edovum* female when brought into contact with at least 20 eggs may be governed by 4 (or perhaps even more) chemical signals, namely: 1) a kairomone present on the chorion of the CPB egg which attracts the parasitoid female so much so that, at times, the female attempts to puncture the substrate to which the eggs had previously adhered; 2) a substance released by the female on the egg by tapping following on behavior A or by other means, signalling that the egg has already been visited; 3) a signal released on the surface of the CPB egg (marking) indicating that the egg has already been parasitized; 4) a substance released inside the egg upon parasitization as a reinforcement of the "already parasitized" signal. This latter signal has been hypothesized as it was observed that after having oviposited in a dozen host eggs the female explores the egg mass, stinging and quickly withdrawing the ovipositor (behavior C), laying its egg only when it finds an unparasitized egg.

In an attempt to evaluate the accuracy with which the "engaged" egg signal is detected by the female, it was observed that detection is all the less regular the lower the number of available eggs, that is, in general, superparasitization is all the more frequent the lower the number of host eggs available. If only one female is left in contact with an egg mass comprising at least 20 to 25 eggs for about 2 hours, the percentage of CPB eggs which receive behavior B twice is, as already stated, in the order of 0.75%. When, however, more than one female are simultaneously active on the same egg mass comprising only 8 to 10 eggs, in addition to the irritation exhibited by the females, the percentage of repeated behaviors B on the same egg is seen to increase. In all cases of superparasitization only one *Edo-*

vum emerges and only on condition that the females have been placed in contact with a few eggs for a long period. This low emergence rate is probably due to the excess of stinging, which therefore also increases the mortality rate of the developing *Edovum*. This may be ascribable either to a concentration of the poison introduced by the parasitoid female into the host egg such as to inhibit its development or to an intraspecific competition amongst *Edovum* females.

The various issues concerning superparasitization in general have been dealt with exhaustively by Van Alphen (1990). As far as *Edovum* is concerned, this topic shall be discussed in a forthcoming paper by Gardenghi *et al.* (1994).

IV. Comparative analysis

Several differences and similarities in the behavior of *Edovum puttleri* and other parasitoid Hymenoptera of the same or of other families are worth noting. Studies conducted by Salt (1937) on *Trichogramma evanescens* (Hym. Trichogrammatidae) showed that the female is capable of distinguishing the eggs walked over by another female thanks to a particular rather volatile substance released by the tarsal glands on the surface of the egg and detected by means of its antennae. This substance would seem to have an inhibitory effect, protecting the eggs for several hours against further attacks, while the signal indicating that the egg has already been parasitized would seem to be given by another substance introduced into the host egg by means of the ovipositor. As with *Edovum*, it would therefore appear that the "parasitized egg" message intended to avoid superparasitization is given by two signals, one of which external and the other internal. Futhermore, as far as *Trichogramma* is concerned, no clear marking behavior was reported. It may therefore be concluded that overall the behavior of the *Edovum* female is more flexible than that of *Trichogramma* as the former feeds on the host even after it has been parasitized.

In his observation of *Diglyphus minoeus* (Hym. Eulophidae), a parasitoid of the leaf miner larva, *Phytomyza lonicerae* (Dipt. Agromizidae), Katò (1989) describes the following behavioral sequence: drumming (which he calls "probing"), introduction of the ovipositor (which according to the author involves the injection of poison into the host), and feeding on the host haemolymph secreted through the puncture ("host feeding"). He further observed that, like *Edovum*, *Diglyphus* refuses eggs which have already been parasitized.

Another Eulophidae, *Tetrastichus asparagi*, a gregarious oophagous parasitoid of *Crioceris asparagi* (Col. Chrysomelidae), feeds on the freshly lain eggs of its host, while ovipositing in eggs containing embryos at an advanced stage of development. According to Van Alphen (1980), while stinging the egg for feeding, the female vigorously stirs the yolk similarly to *Edovum*, while it remains still for several minutes with the ovipositor inside the egg during parasitization, recognizing whether the host has already been parasitized. The author suggests that the eggs are marked both externally and internally (albeit the latter marking is not evident) and that these are then recognized as having been parasitized by external drumming and by internal probing with the ovipositor. *Tetrastichus gallerucae* also exhibits a similar behavior to that of *T. asparagi*, but, as in *Edovum*, probing is perfor-

med on the same host by more than one female. Even if the marking activity as such is not clearly distinguishable, Hamerski and Hall (1989) have suggested that it nevertheless takes place during the behavioral sequence as a whole.

The behavioral sequence of *Encarsia formosa* (Hym. Aphelinidae), employed in the greenhouse biocontrol of *Trialeurodes vaporariorum* (Hom. Aleyrodidae), is similar to those already described and the parasitoid is also capable of distinguishing the developmental stages of the host, thus avoiding to parasitize the hosts which have already been parasitized. It recognizes the parasitized hosts by means of its antennae, sometimes also probing them with its ovipositor (Van Lenteren *et al.*, 1976, 1980) so that both an external and internal marking would seem to be operating. Unlike *Edovum*, however, *Encarsia* females do not feed on the already parasitized hosts.

Other parasitoids exhibiting a similar behavioral sequence to that of *Edovum* are *Telenomus nitidulus* (Hym. Scelionidae), an oophagous parasitoid of *Leucoma salicis* (Lep. Lymantriidae) studied by Grijpma and Van Lenteren (1988), and *T. heliothidis* studied by Strand and Vinson (1983). Both these parasitoids mark the host eggs by moving the ovipositor across the surface.

Overall, it may be concluded that the behavior of the various parasitoid Hymenoptera examined, even if belonging to different families, is fairly similar, differences depending on the stage of development of the host upon parasitization and on the ease with which the parasitoid comes into contact with the host. In all cases, the scope of this behavior is the same and fourfold, namely: a) recognition of the host; b) exploitation of the host for feeding; c) giving out of signals for the purpose of preventing superparasitization which would be unproductive for the species; d) preservation of a number of hosts so as to maintain an equilibrium in the host-parasitoid population. These patterns are a sort of adaptive strategy which, also in consideration of the substantial phylogenetic affinity, have led to a considerable similarity in behavior.

SUMMARY

The behavior of *Edovum puttleri* females acting on *Leptinotarsa decemlineata* (CPB) egg masses was studied by direct observation and by videotape recording. Three different behavioral patterns, termed by us A,B, and C, were consistently identified.

Behavior A is characterized by a sequence of actions including boring of the egg, yolk stirring by means of the ovipositor introduced by 3/4 of its length into the host egg, and feeding on the drop of ooplasma flowed out of the hole drilled by the ovipositor. This sequence can be repeated several times on the same host egg.

During behavior B, the female of the parasitoid repeats the first part of behavior A but remains still on the egg with its ovipositor fully inserted for a longer time at the end of which it deposits its egg. After hatching within the host egg, the *Edovum* larva feeds on the ooplasm thus inhibiting the development of the CPB larva. As a rule, behavior B is performed only once on the same egg after which it is abandoned by the female.

Behaviour C is mostly observed in young females or in females at the end of their daily activity. The ovipositor is rapidly introduced into the host egg to about half its length without, however, any yolk stirring or feeding activity. The female usually performs behavior C only once before changing egg.

The fate of host eggs after behavior A may be one of the following: 1) birth of the CPB larva; 2) death of the CPB embryo (abortion); 3) collapse of the host egg without any visible sign of the embryo having developed. Damage to the CPB egg increases as the female proceeds in its daily activity on the egg mass.

Behavior B leads to the emergence of *Edovum* in about 86% of cases. The remaining eggs which

have undergone this treatment may collapse or contain *Edovum* which have perished before emergence. In some cases, the *Edovum* may fail to deposit its egg inside the host (5.48%) in which event, however, the CPB egg always perishes. The fate of CPB eggs which had been subjected to behavior B alone or to behavior B preceded by various behaviors A was also examined.

The effects of behavior C are more damaging when performed by mature females than by newly emerged or very old females.

Il comportamento di *Edovum puttleri* Grissell (Hym. Eulophidae) su uova di *Leptinotarsa decemlineata* (Say) (Col. Chrysomelidae) e studio sul loro destino.

RIASSUNTO

Tramite osservazione diretta e registrazione con videotape è stato studiato il comportamento di femmine di *Edovum puttleri* in attività su ovature di *Leptinotarsa decemlineata* (CPB). Sono stati individuati costantemente 3 diversi comportamenti da noi indicati con le lettere "A" "B", "C".

Il comportamento "A" é realizzato con una sequenza di azioni successive tra cui emergono: perforazione dell'uovo; rimescolamento dell'ooplasma effettuato con l'ovopositore inserito per 3/4 della sua lunghezza nell'uovo ospite; alimentazione a spese della goccia di ooplasma emergente dal foro praticato. Questo comportamento può essere ripetuto più volte sullo stesso uovo.

Durante il comportamento "B" la femmina del parassitoide ripete la prima parte del comportamento "A" ma si ferma più a lungo con l'ovopositore inserito per tutta la sua lunghezza nell'uovo ospite e alla fine vi depone il proprio uovo. La larva di *Edovum* schiusa all'interno dell'uovo ospite si nutre a spese dell'ooplasma inibendo lo sviluppo della larva di CPB. Di regola la femmina effettua una sola sequenza comportamentale "B" sullo stesso uovo e poi si allontana da esso.

Il comportamento "C" si osserva soprattutto in femmine giovani o alla fine della loro attività giornaliera. Esso consiste in una rapida immissione dell'ovopositore per circa la metà della sua lunghezza nell'uovo di *Leptinotarsa* senza che vi siano però rimescolamento dell'ooplasma ed alimentazione. Solitamente la femmina effettua un solo comportamento "C" e poi cambia uovo.

Dopo il comportamento "A" si può avere: 1) la nascita della larva di CPB; 2) la morte dell'embrione di CPB; 3) il collasso dell'uovo ospite senza che vi sia alcuno sviluppo embrionale visibile. Il danno alle uova di CPB é più grave man mano che la femmina procede nella sua attività sull'ovatura.

Gli effetti del comportamento "B" sono lo sfarfallamento di *Edovum* nel 86 % circa delle uova che lo hanno subito; le restanti uova interessate da tale comportamento possono collassare oppure contenere degli *Edovum* morti prima di sfarfallare. La ovideposizione di *Edovum* può anche fallire (5,48%) ma dopo l'uovo di CPB muore sempre. E' stato esaminato il destino delle uova di CPB che hanno subito il comportamento "B" da solo o preceduto da vari comportamenti "A".

Gli effetti del comportamento "C" eseguiti da femmine mature, sono più gravi di quelli eseguiti da femmine da poco sfarfallate o molto vecchie.

Key words: Eulophidae, *Edovum* behavior, host fate.

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