Entomol. exp. appl. **61**: 139–147, 1991.

Oviposition behavior of *Edovum puttleri*, reared on two hosts, *Leptinotarsa decemlineata* and *L. texana*

J. E. Corrigan*, J. H. Lashomb, M. L. May & C. Schal
*Department of Entomology, New Jersey Agricultural Experiment Station, Rutgers University, New Brunswick, N.J. 08903, USA; *Present address: Dept. of Environmental Biology, University of Guelph, Guelph Ont., Canada N1G 2W1*

Accepted: June 3, 1991

Key words: Edovum puttleri, Leptinotarsa decemlineata, Leptinotarsa texana, oviposition behavior, parasitoid behavior, host feeding

Abstract

Female *Edovum puttleri* Grissell [Hymenoptera: Eulophidae], reared from eggs of *Leptinotarsa decemlineata* (Say) or *Leptinotarsa texana* Schaeffer [Coleoptera: Chrysomelidae], were videotaped as they attacked egg masses of *L. decemlineata* containing 20 host eggs. We identified 15 components of ovipositional behavior. Parasitoids reared on *L. texana* attacked and oviposited in significantly more host eggs than did females reared on *L. decemlineata*. Ethometric analyses of behavioral transitions and a clustering analysis of 34 behavioral parameters showed that females reared on *L. texana* attacked the host egg mass in a different manner than those reared from *L. decemlineata*. It was concluded that differences were associated with the host species upon which they were reared. Contrary to previous reports, mortality of unparasitized hosts was caused by an ovipositor probe of short duration, which was not related to host-feeding.

Introduction

Edovum puttleri Grissell [Hymenoptera: Eulophidae] is a solitary egg parasitoid of beetles of the genus *Leptinotarsa* [Coleoptera: Chrysomelidae]. It was collected in Colombia (Puttler & Long, 1983), and Mexico (Logan *et al.*, 1987) and imported to North America as a potential control agent for *L. decemlineata* (Say), the Colorado potato beetle (Schroder & Athanas, 1985). In mass rearing programs, *E. puttleri* has been reared from eggs of both *L. decemlineata* and *L. texana* Schaeffer. Parasitoids reared from the larger eggs of *L. texana* are significantly larger than those produced from the smaller *L. decemlineata* eggs, and are capable of parasitizing significantly more hosts when presented with a single *L. decemlineata* egg mass (Corrigan & Lashomb, 1990).

The objectives of this study were to identify the components of the oviposition sequence of *E. puttleri*, to show how they are integrated into attacks on each *L. decemlineata* host egg in a mass of 20 eggs, and on the entire egg mass. These experiments will provide base line data needed for further studies of the evolutionary significance of superparasitism and host killing without parasitism. The study also compares the oviposition behavior of females reared from each host species.

This information is relevant to biological pest control, as natural enemies used in inundative release programs are often reared on other host species in the laboratory.

Materials and methods

The parasitoids originated from the Colombian population imported by Puttler and Long (1983). Pupal *E. puttleri*, reared on eggs of *L. texana*, were obtained from the USDA-APHIS Biological Control Laboratory in Mission, Texas. They came from a single, freely-mixing population reared on both *L. decemlineata* and *L. texana* (G. Bernon, pers. comm.). In the following experiments, 29 females reared on *L. texana* and 9 females reared on *L. decemlineata*, all from the Texas population, were compared with 51 females reared on *L. decemlineata* in our laboratory.

Prior to the experiments, adult wasps were held at 26 ± 1 °C, 60–70% r.h., L16:D8 h and had constant access to water and undiluted honey. Because females of *E. puttleri* have an intensive egg laying period between 4 and 16 days post-eclosion (Corrigan & Lashomb, 1990), all females used in experiments were 7–15 days old. They were exposed to *L. decemlineata* egg masses to gain parasitization experience, but were denied access to hosts for 48 h before experiments to ensure that they had not depleted their supply of eggs immediately before a trial. Ovary dissections showed that *E. puttleri* develop a full clutch of eggs within 48 h after oviposition (Corrigan & Lashomb, 1990).

Experiments were conducted between 7 h and 13 h after lights-on (1400–2000 h EST), at 29 ± 2 °C and variable humidity. All egg masses were produced by *L. decemlineata* fed on greenhouse-grown potato (*Solanum tuberosum* L. var. 'Superior'), and were less than 28 h old. A leaf disc containing an egg mass with 20 eggs was attached to the middle of a 9 cm petri dish using a small drop of white, non-toxic glue. Five to ten female *E. puttleri* were introduced into each petri dish. When the first female walked onto the egg mass, all others were quickly removed. The female was continuously videotaped from the time she discovered the egg mass until she left and remained off the egg mass for 30 min.. Each attacked egg was placed in a gelatin capsule and incubated at 26 ± 1 °C and 60–70% r.h.. To measure host mortality without parasitoid attack, unattacked eggs from the trials were monitored for emergence of beetle larvae, and ten egg masses were set up without exposure to parasitoid attack.

The duration and sequential position of every behavioral act was transcribed to a computer file for analysis. We were unable to use Markov chain models (Slater, 1973; Fagen & Young, 1978) because transition probabilities changed radically throughout the trial period. For this reason, we created probabilistic flow diagrams (Sustare, 1978) to illustrate 'typical' attacks for parasitoids reared from each host species. Transition matrices were formed by pairing successive behavioral acts. Antennal drumming/walking was excluded from the matrices as it occurred between every incidence of all other components. Other behaviors were delineated for timing purposes by the onset and termination of drumming/walking. The data were pooled and sorted with respect to the order of the attack in the trial period (1st attacks by all parasitoids, 2nd attacks, etc.). Fifty-one trials were available for females reared on *L. decemlineata*, so a hierarchical agglomerative clustering procedure (complete linkage, SAS Institute, 1985) was used to identify those attacks that were most similar to each other, based on the frequency of occurrence of each transition within an attack. The attacks falling into each of the final three bifurcations were lumped together for illustrative purposes. Attacks by *L. texana* were grouped in an identical manner to permit direct comparisons of the two groups.

Definitions: A *behavioral component* is a discrete type of activity, recognized by characteristic posture, duration and temporal position relative to other behaviors in the oviposition sequence. Any behavioral component that involved an attempted or successful drilling of the host's chorion is a *probe*. All behavioral components occurring with a probe, from the time the parasitoid walked onto the host egg until she left it, are part of the *attack*

on that host. More than one probe could occur within a single attack and a host could be attacked more than once at different times during the *trial period*, the interval from the female's first contact with the egg mass until she left the mass for the final time.

Means and distributional data were compared with *t*-tests (SAS Institute, 1985) and 2-sample Kolmogorov-Smirnov test (Sokal & Rohlf, 1981) respectively. The level accepted for rejection of the null hypothesis was 0.05; standard deviations are reported as measures of variation for all means. Other statistical procedures are described below.

Results and discussion

In 89 trials, over 270 h of activity were recorded and 40,166 behavioral acts were observed. Fagen and Goldman (1977) developed the sample coverage statistic, θ, which estimates the degree that a given sample of behavioral observations contains all behaviors of a particular repertoire. In our trials, the sample coverage estimate was equal to 1, suggesting that all behavioral components associated with oviposition were observed in these experiments. Fifteen behavioral components were identified. All components were performed by females from all three groups except for 'vibrating', which was only performed twice by one *L. texana* female (Table 1).

The two experimental groups from Texas were identical with respect to genetic background, rearing and shipping conditions, differing only in host species. Because one of these groups shared the same host species (*L. decemlineata*) with parasitoids reared in our laboratory, it was possible to determine if observed behavioral differences might be associated with the host species, or with different genetic, rearing and shipping conditions experienced by the New Jersey and Texas populations.

Mean values for variables derived from the 15 behavioral components were calculated for each group, producing a three (*E. puttleri* group) × 34 (variables) matrix. The relative similarities of the three groups were compared using hierarchical agglomerative clustering procedures (SAS Institute, 1985). Four clustering algorithms (i. single linkage, ii. complete linkage, iii. average linkage [UPGMA], iv. centroid linkage [UPGMC]), were used on untransformed data and on data with variables standardized to a mean of 0 and a standard deviation of 1. All eight clustering procedures showed that the two groups reared on *L. decemlineata* in New Jersey and Texas were more similar to each other than either group was to *L. texana*-reared parasitoids. These results suggest that rearing or shipping conditions were less important than the host species with respect to the behavioral differences observed between parasitoid groups, so in the rest of the paper we compare parasitoids reared on *L. texana* with those reared on *L. decemlineata* in our laboratory.

Females reared on *L. texana* performed significantly more attacks per egg mass, and oviposited in significantly more eggs than females reared on

Table 1. The frequency of components of ovipositional behavior in *E. puttleri* (descriptions in text)

Behavioral component	Number of observations
Components performed while standing in place	
Vibrating body*	2
Legs straight/ovipositor exerted	10
Grooming body with legs	219
Standing still	2833
Components performed while in motion	
Antennal drumming/walking	29174
Walking/flying off egg mass	575
Dragging abdomen tip on chorion	342
Probes	
Drilling chorion**	127
Quiescent probe	17
Oviposition	1264
Long probe	499
Quick probe	282
Short probe	420
Host-feeding	2601
Tapping chorion with abdomen tip	1801

* Observed in one female reared on *L. texana*.

** Drilling was associated with all probes. These observations refer to drilling not followed by another probe.

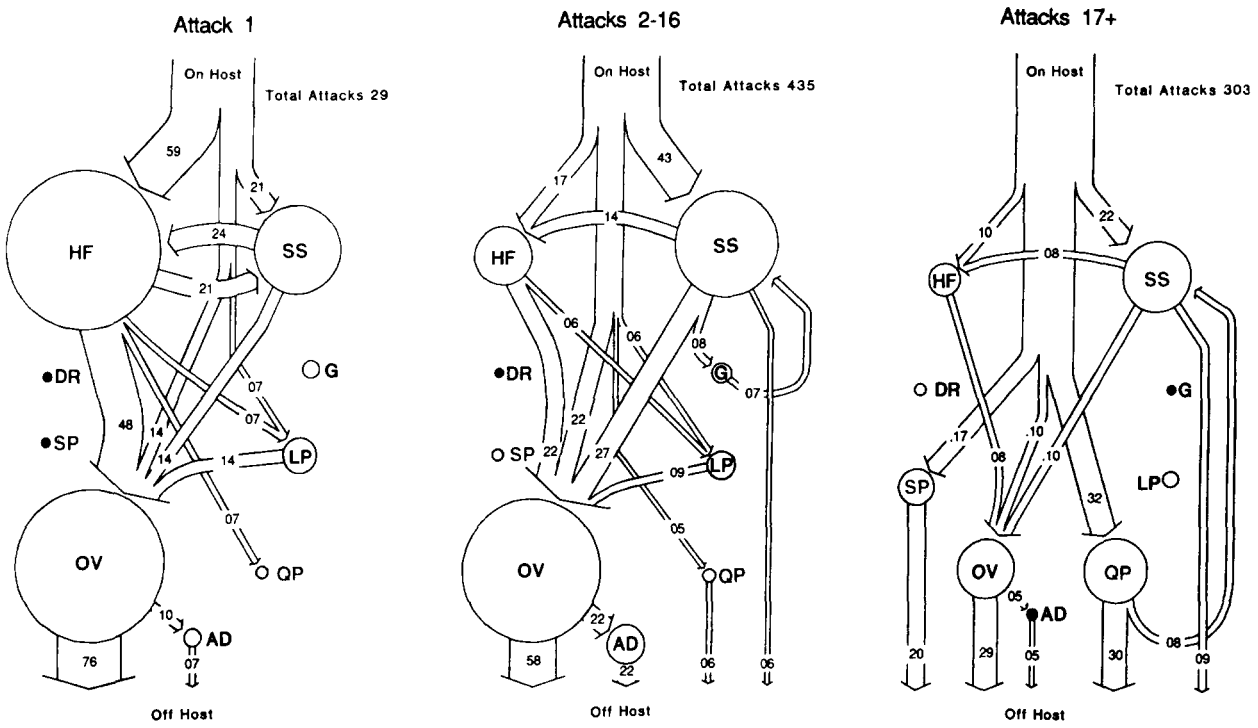

Fig. 1. 'Typical' attacks for females reared from *L. texana*. Width of vectors and numbers represent the proportion of all transitions occurring between two components. Transitions occurring with frequency less than 0.05 are not illustrated. Radius of circle represents relative frequency of transitions passing through that component. Black dots represent components with 0.05 or less of the transitions passing through tem. AD = abdominal dragging, DR = drilling, G = grooming, HF = host-feeding, SP = short probe, LP = long probe, OV = oviposition, SS = standing still, QP = quick probe.

L. decemlineata, however the total time on the egg mass was not significantly different between the two groups (Table 2). Significantly fewer beetle larvae emerged from the egg masses attacked by *L. texana*-reared females than from those attacked by *L. decemlineata*-reared females (Table 2).

Sequential patterns of oviposition behavior

The clustering procedure for attacks by females reared on *L. decemlineata* produced the following groups: i all first attacks; ii attacks 2–16; iii attacks 17+. Figures 1 and 2 present three probabilistic flow diagrams of 'typical' early, middle

Table 2. Ovipositional performance (mean ± SD) per female of *E. puttleri* on an egg mass of *L. decemlineata* containing 20 eggs

Rearing host species	Total number of attacks	Number of ovipositions	Number of surviving beetle larvae	Time on egg mass (hours)
L. texana	26.4 ± 6.8	17.1 ± 2.2	0.6 ± 0.9	3.1 ± 0.6
L. decem.	21.3 ± 4.5	12.8 ± 2.8	2.2 ± 2.7	3.0 ± 0.8
	T = 3.64	T = 7.02	T = 3.76	T = 0.28
	df = 78	df = 78	df = 78	df = 73*
	P < 0.001	P < 0.001	P < 0.001	P = 0.89

* Total times not available for 5 females.

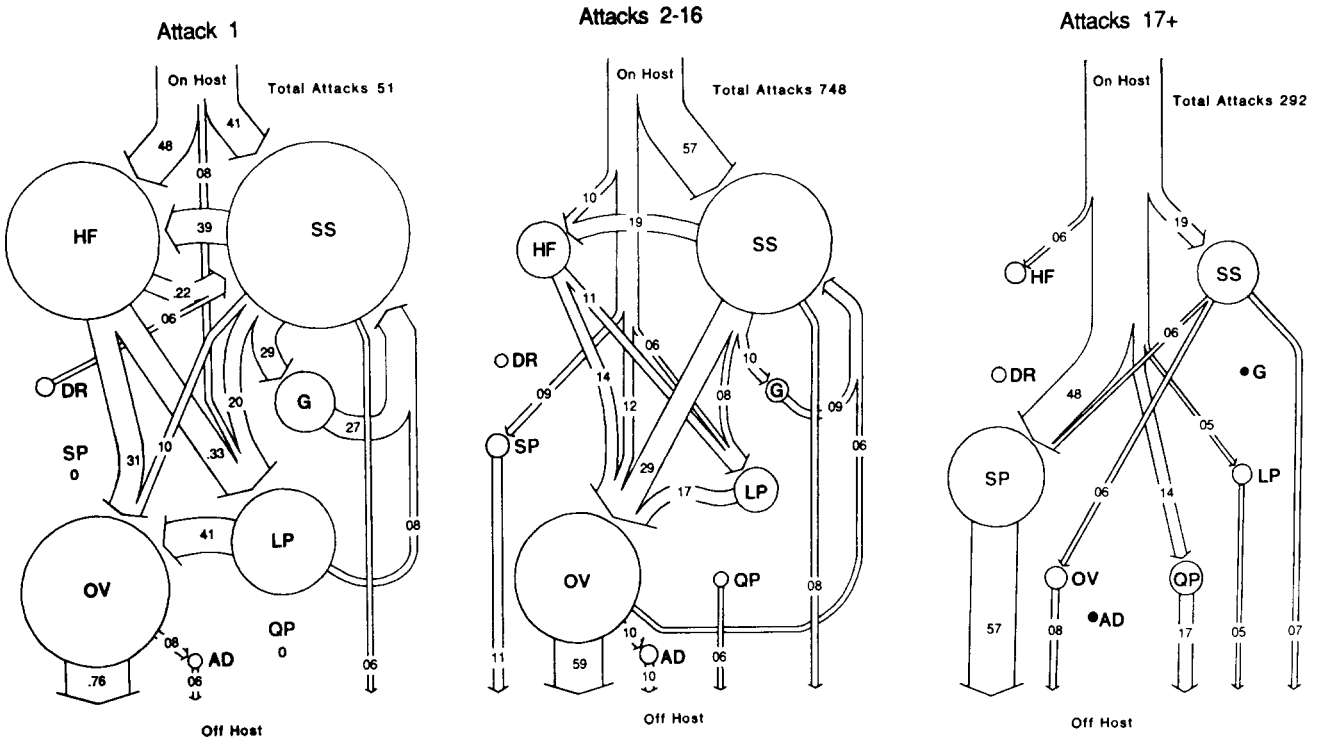

Fig. 2. 'Typical' attacks for females reared from *L. decemlineata*. All symbols and rules of construction are identical to those used in Figure 1.

and late attacks for female parasitoids reared on *L. texana* and *L. decemlineata*, respectively. The width of each vector represents the frequency of that transition relative to the total number of transitions in the diagram. Input does not exactly equal output at some nodes, as any transition that occurred below a 5% frequency was not included. Nine components are illustrated. Vibrating, legs straight/ovipositor exerted, and the quiescent probe are not illustrated because of their rarity. Host-feeding events occurred in series or bouts, alternating irregularly with tapping. Host feeding bouts, not the number of individual host-feeding events, are illustrated. Self-transitions (e.g. long probe to long probe) are not illustrated.

In a typical first attack, females reared on *L. decemlineata* were more likely to stand still, groom, and perform long probes than females reared on *L. texana* (Figs. 1, 2). Attacks 2–16 appeared to be similar in both groups, although females from *L. decemlineata* did more short probes and females reared on *L. texana* did more abdomen drags. In attacks 17+, females reared on *L. decemlineata* rarely oviposited; their dominant probe was the short probe, however females reared on *L. texana* were more likely to oviposit or perform a quick probe than a short probe (Figs. 1, 2).

In both groups, early attacks usually terminated with oviposition, and the likelihood of an attack including oviposition decreased through the trial period (Fig. 3). However, females reared on *L. texana* interspersed significantly more attacks without oviposition (5.6 ± 5.7) among their ovipositional attacks than did females reared on *L. decemlineata* (2.1 ± 2.8) (*t*-test, $T = 3.07$, $df = 87$, $P = 0.01$). Females reared on *L. texana* took significantly less time to complete an oviposition (66.3 ± 23.1 s) than females from *L. decemlineata* (76.0 ± 25.3 s) (*t*-test, $T = 6.71$, $df = 1103$, $P < 0.001$).

When performing a 'long' probe, a parasitoid inserted approximately 75% of the length of her ovipositor into the host. The entrance hole acted

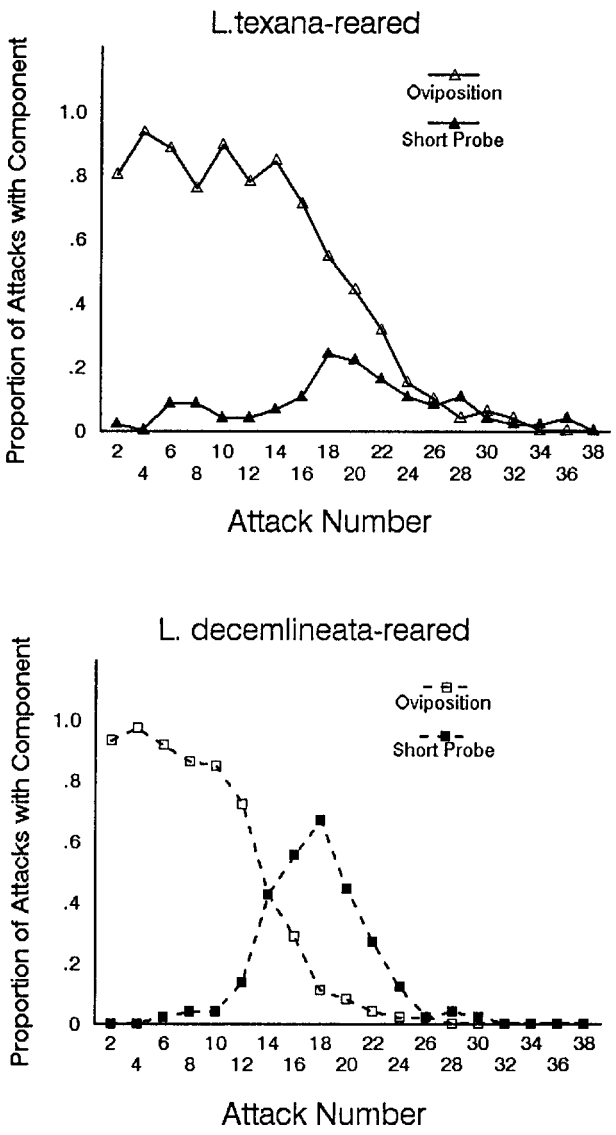

Fig. 3. Proportion of *L. texana*-reared and *L. decemlineata*-reared females performing ovipositions and short probes through the trial period.

as a fulcrum; by moving her abdomen, she whipped the ovipositor about inside the host egg. The number of long probes performed per trial period was not significantly different between groups (*L. texana* 3.9 ± 4.2; *L. decemlineata* 6.2 ± 6.6) (*t*-test, T = 1.89, df = 78, $P = 0.097$), but females reared on *L. decemlineata* performed significantly more long probes early in the trial period (Kolmogorov-Smirnov test, $D_{max} = 0.59$, $P < 0.05$) (Fig. 4). A long probe was shorter in duration for females from *L. texana* than for females from *L. decemlineata* (26.4 ± 8.6 s vs. 30.3 ± 9.4 s) (*t*-test, T = 3.87, df = 424, $P < 0.001$).

We conclude that long probes were not used to kill hosts or to detect previously parasitized hosts. Long probes usually occurred immediately before oviposition (Figs. 1, 2), and were rarely performed on unparasitized host eggs. They were rarely observed late in trial periods when one would expect behavior associated with the recognition of previously attacked hosts (Figs. 1, 2).

Female *E. puttleri* generally avoided probing a previously parasitized host, rejecting it after antennal drumming. If they did attack a parasitized host, they usually performed a 'quick' probe then left the host. In this probe, the ovipositor tip was in contact with the chorion for less than 2 sec. after initial ovipositor contact, and the ovipositor did not appear to pierce the chorion. The quick probe was performed significantly more frequently in the trial period by females reared on *L. texana* (5.1 ± 5.2) than by females reared on *L. decemlineata* (2.3 ± 2.7) (*t*-test, T = 2.75, df = 78, $P < 0.001$).

In several parasitoid species, previously parasitized hosts are often abandoned after a drilling period of normal length, possibly without the chorion being pierced (Salt, 1938; Klomp *et al.*, 1980; Narendan, 1985). Similarly, *E. puttleri* may use the quick probe to determine if the host has been previously attacked. The frequency of quick probes increased late in the trial period when many hosts had already been attacked (Fig. 5), and they were usually the only probe performed in these attacks (*L. texana* 95%, *L. decemlineata* 92%). Quick probes rarely were performed as part of the first attack on a host (*L. texana* 10%, *L. decemlineata* 31%), and were rarely the only probe used on a host egg during the trial period (*L. texana* 3%, *L. decemlineata* 16%).

When host-feeding, a parasitoid typically drills the chorion, inserts about 20% of her ovipositor, and then performs a rapid lateral rocking motion which moves the ovipositor tip back and forth in the host egg. She then quickly withdraws her ovipositor, moves backward, and drinks the host fluid that exudes from the drill hole. Females

reared on *L. texana* fed upon significantly more hosts (7.3 ± 2.5) in the trial period than did females from *L. decemlineata* (5.8 ± 1.9) (*t*-test, $T = -3.08$, $df = 78$, $P < 0.01$).

For several parasitoid species, host-feeding kills many unparasitized hosts (*Tetrastichus asparagi* Johnson, 1915, cited *in* DeBach, 1943; *Metaphycus helvolus* DeBach, 1943; *Coccophagus bartletti* Walter, 1988). Previous studies of *E. puttleri* attributed non-parasitism mortality to host-feeding (Schroder & Athanas, 1985; Lashomb *et al.*, 1987; Ruberson *et al.*, 1987, 1988), but we did not find host-feeding to be responsible for the mortality of non-parasitized hosts. Host-feeding occurs almost exclusively before oviposition in the attack sequence (Figs. 1, 2) and almost always on hosts that are parasitized (*L. texana* 94%, *L. decemlineata* 88%). In only four cases was host-feeding the only probe preformed on a host during the trial period (*L. texana* 1%, *L. decemlineata* 2%), and in two of these cases a beetle larvae emerged from the attacked egg.

Female *E. puttleri* kill hosts with a probe of short duration ('short' probe – *L. texana*-reared, 16.2 ± 2.8 s, *L. decemlineata*-reared, 15.7 ± 2.4 s) in which about 50% of the ovipositor is inserted in the host. The ovipositor enters and leaves the host in a virtually continuous motion. For females from *L. decemlineata*, the frequency of short probes increased as oviposition declined, giving their trial periods as bi-phasic appearance (Figs. 2, 3). Females from *L. texana* performed significantly fewer short probes than females from *L. decemlineata* (2.9 ± 2.5 vs. 5.3 ± 2.9) (*t*-test, $T = 2.93$, $df = 78$, $P < 0.001$) and did not appear to concentrate these attacks in a particular part of the trial period (Figs. 1, 3), being more likely to oviposit in hosts that had already received a short probe.

Observed mortality of unattacked hosts in the trials was 7% ($N = 128$ host eggs), and 8% ($\pm 10\%$) in the ten egg masses not exposed to attack by the parasitoids, so we are confident that the vast majority of mortality of non-parasitized eggs was due to the action of the parasitoids. Correlation of the occurrence of short probes with the fate of host eggs indicates that this probe is

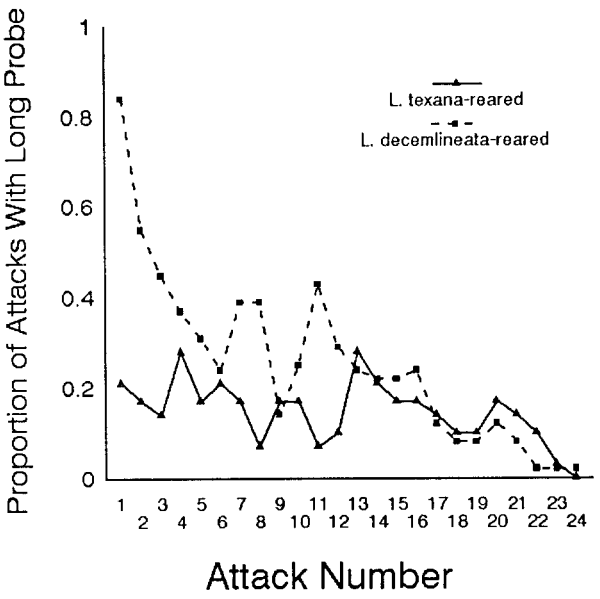

Fig. 4. Proportion of females performing the long probe through the trial period. The distributions of this component were significantly different between *L. decemlineata*-reared females (Kolmogorov-Smirnov test, $D_{max} = 0.591$, $P < 0.05$).

responsible for mortality of unparasitized hosts. Sixty-six and 34% of the short probes performed by *L. decemlineata* and *L. texana*-reared females, respectively, were the only probes performed on hosts during the trial period (Figs. 1, 2), and mortality of these eggs was very high (*L. decemlineata* 94%, *L. texana* 97%).

In a typical abdominal drag, a walking female lowers the tip of her abdomen to the surface of the egg and pulls it ventrally under her body and along the chorion. For those females performing at least one abdominal drag, females from *L. texana* did so on significantly more hosts (7.3 ± 3.4) than females from *L. decemlineata* (4.1 ± 3.1) (*t*-test, $T = 3.01$; $df = 37$, $P < 0.01$).

Rabb and Bradley (1970) found that 99% of the hosts marked by the scelionid egg parasitoid *Telenomus sphingis* contained a parasitoid egg, while only 15% of unmarked eggs were parasitized. They concluded that the mark was deposited to discourage further oviposition in the host. For *E. puttleri*, the sequential placement of an abdominal drag after oviposition (Figs. 1, 2) suggests the deposition of a mark to facilitate host

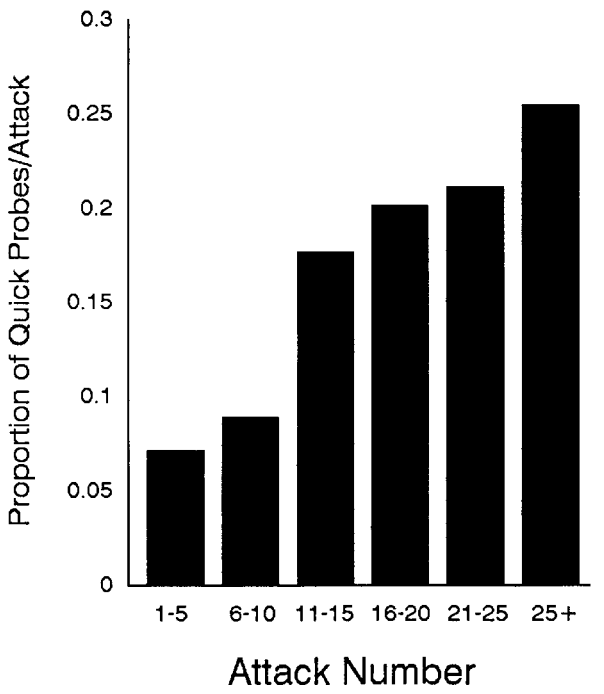

Fig. 5. Incidence of the quick probe at different points through the trial period for all parasitoids.

discrimination. However, about 50% of the females did not do abdominal drags (*L. texana* 45%, *L. decemlineata* 55%). For those females performing at least one abdominal drag, over half of their ovipositions were not followed by this behavior (*L. texana*-reared 58%, *L. decemlineata*-reared 69%, Figs. 1, 2). Moreover, only six incidents of superparasitism occurred in 1264 ovipositions. It appears that females can recognize a previously parasitized host whether it is 'marked' by an abdominal drag or not.

Some of the observed behavioral differences between parasitoids reared from *L. texana* or *L. decemlineata* may be a consequence of host size effects on parasitoid physiology. Larger parasitoids were produced from the larger egg of *L. texana*, and they could produce more progeny on an egg mass (Corrigan & Lashomb, 1990). With a higher proportion of the 20-host egg mass parasitized, wasps reared on *L. texana* needed to perform more probes investigating the parasitization status of a host (quick probe) and fewer probes to kill unparasitized eggs (short probe) than wasps from *L. decemlineata*. In order to develop more eggs, females reared from *L. texana* probably had to feed on more hosts. Despite this, there were behavioral differences that did not obviously relate to differences in reproductive performance. For example, females reared from *L. texana* took less time to complete long probes or ovipositions. They interrupted sequences of ovipositional attacks more frequently with non-ovipositional attacks. They distributed their long probes differently through the trial period, spent less time standing still, and performed more abdominal drags than females reared on *L. decemlineata*. Although many differences in the ovipositional behavior of *E. puttleri* from the two hosts may be simply due to differences in host size, there are some differences that might not be expected based solely on size-related attributes.

Parasitoids reared from different host species may vary significantly for non-behavioral parameters such as longevity, fecundity and size (Boldt & Marston, 1974; Lewis *et al.*, 1976; van Vianen & van Lenteren, 1982, cited *in* van Lenteren, 1986; Corrigan & Lashomb, 1990). Our results show that ovipositional behavior is also influenced by the host upon which it is reared. This must be considered when using behavioral responses in bioassays of host quality of kairomonal activity. Moreover, behavioral differences associated with oviposition, as well as those associated with host location and discrimination, must be investigated when parasitoids produced from alternate host species are considered for use in biological control programs.

Acknowledgements

We thank J. Hwang and A. Zitzman for technical assistance and R. Bennett, E. Burns and J. Laing for reviewing the manuscript. We are indebted to the Mission Biological Control Laboratory for shipments of parasitoids. This study was supported by the U.S.D.A. under agreement 58-32U4-6-13, IPM Pilot Tests, U.S.D.A. 86-CRSR-2-2773. New Jersey Agricultural Experiment Station Publication Number D-08240-06-

89, supported by State funds and by the U.S. Hatch Act.

References

Boldt, P. E. & N. Marston, 1974. Eggs of the greater wax moth as a host for *Trichogramma*. Environ. Entomol. 3: 545–548.

Corrigan, J. E. & J. H. Lashomb, 1990. Host influences of the bionomics of *Edovum puttleri*: effects on size and reproduction. Environ. Entomol. 19: 1496–1502.

DeBach, P., 1943. The importance of host-feeding by adult parasites in the reduction of host populations. J. Econ. Entomol. 36: 647–658.

Fagen, R. M. & R. N. Goldman, 1977. Behavioral catalogue analyses methods. Anim. Behav. 25: 261–274.

Fagen, R. M. & D. Y. Young, 1978. Temporal patterns of behaviors: durations, intervals, latencies, and sequences. pp 79–114. *In* P. W. Colgan (ed), Quantitative Ethology. John Wiley and Sons, New York.

Johnson, F. A., 1915. Asparagus-beetle egg parasite. J. Agric. Res. 4: 303–313.

Klomp, H., B. J. Teerink & W. C. Ma, 1980. Discrimination between parasitized and unparasitized hosts in the egg parasite *Trichogramma embryophagum* (Hym: Trichogrammatidae): a matter of learning and forgetting. Neth. J. Zool. 30: 254–277.

Lashomb, J. H., J. D. Krainacker, R. K. Jansson, Y. S. Ng & R. Chianese, 1987. Parasitism of *Leptinotarsa decemlineata* (Say) eggs by *Edovum puttleri* Grissell (Hymenoptera: Eulophidae): effects of host age, parasitoid age, and temperature. Can. Entomol. 119: 75–82.

Lenteren, J. C. van, 1986. Evaluation, mass production, quality control and release of entomophagous insects. pp 31–56. *In* J. M. Franz (Ed) Biological Plant and Health Protection. Fischer, Stuttgart.

Lewis, W. J., D. A. Nordlund, H. R. Gross, Jr., W. D. Perkins, E. F. Knipling & J. Voegele, 1976. Production and performance of *Trichogramma* reared on eggs of *Heliothis zea* and other hosts. Environ. Entomol. 5: 449–452.

Logan, P. A., R. A. Casagrande, T. H. Hsiao & F. A. Drummond, 1987. Collections of natural enemies of *Leptinotarsa decemlineata* [Coleoptera: Chrysomelidae] in Mexico. 1980–1985. Entomophaga 32: 249–254.

Narendran, T. C., 1985. Analyses of superparasitic behavior and host discrimination of chalcid wasps (Hymenoptera: Chalcidoidea). Proc. Indian Acad. Sci. 94: 325–331.

Puttler, B. & S. H. Long, 1983. Host specificity tests of an egg parasite, *Edovum puttleri* (Hymenoptera: Eulophidae), of the Colorado potato beetle, *Leptinotarsa decemlineata* (Coleoptera: Chrysomelidae). Proc. Entomol. Soc. Wash. 85: 384–387.

Rabb, R. L. & J. R. Bradley, 1970. Marking host eggs by *Telonomus sphingis*. Ann. Entomol. Soc. Amer. 71: 92–94.

Ruberson, J. R., M. J. Tauber & C. A. Tauber, 1987. Biotypes of *Edovum puttleri* Grissell (Hymenoptera: Eulophidae): responses to developing eggs of the Colorado potato beetle. Ann. Entomol. Soc. Amer. 80: 451–455.

Ruberson, J. R., M. J. Tauber & C. A. Tauber, 1988. Reproductive biology of two biotypes of *Edovum puttleri*, a parasitoid of Colorado potato beetle eggs. Entomol. exp. appl. 46: 211–219.

Salt, G., 1938. Experimental studies in insect parasitism. VI. host suitability. Bull. Entomol. Res. 29: 223–246.

SAS Institute, 1985. SAS/STAT Guide for Personal Computers: Version 6 Edition. SAS Institute, Cary, N.C.

Schroder, R. F. & M. M. Athanas, 1985. Review of research on *Edovum puttleri* Grissell, egg parasite of the Colorado potato beetle. pp 29–32. *In* D. N. Ferro and R. H. Voss (eds) Proceedings of the Symposium on the Colorado Potato Beetle. Massachusetts Experimental Station, Amherst, Mass.

Slater, P. J. B., 1973. Describing sequences of behavior. Perspectives in Ethology 1: 131–153.

Sokal, R. R. & F. J. Rohlf, 1981. Biometry, 2nd Edition. Freeman, New York.

Sustare, D. B., 1978. Systems diagrams. pp 275–311. *In* P. W. Colgan (ed) Quantitative Ethology. John Wiley and Sons, New York.

Vianen, A. van & J. C. van Lenteren, 1982. Increasing the number of ovarioles of *Encarsia formosa* – a possibility to improve the parasite for biological control of the greenhouse whitefly, *Trialeurodes vaporariorum*? Med. Fac. Landbouww. Rijksuniv. Gent 47: 523–531.

Walter, G. H., 1988. Activity patterns and egg production in *Coccophagus bartletti*, an aphelinid parasitoid of scale insects. Ecol. Entomol. 13: 95–105.