

HOST-PLANT EFFECTS ON THE BEHAVIOR OF *ERETMOCERUS* SP. NR. *CALIFORNICUS* FEMALES RAISED FROM MELON

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The behaviors of female *Eretmocerus* sp. nr. *californicus* raised from *Bemisia argentifolii* Bellows & Perring on melon, *Cucumis melo* L., were analysed on four different host plant species (cotton, melon, sweet potato and *Abutilon theophrasti* Medic.). Comparison with previously published results of similarly treated females reared from sweet potato plants showed performance related differences leading to oviposition. In the present study, the generalized behavioral pathway (walking, host-encounter, antennation, probing and oviposition) did not vary among host plant species for melon-reared parasitoid females. Host assessment by antennation leading to host acceptance for probing varied from 10.5-12.3 sec among the host plant species with no host stage-related differences in duration. Initial and repeated (multiple probes on the same host nymph) probing events varied from 52.4 to 77.3 sec among host plant species and no stage-related differences were detected. Oviposition occurred under 62 % of the nymphs on cotton, 100 % of the nymphs on melon and 51 % of the nymphs on sweet potato under which the ovipositor was exerted. On cotton, melon and sweet potato proportionally fewer first instar nymphs were encountered than present, a larger proportion of the second instars that were encountered were subsequently antennated, and a larger proportion of second instars on cotton were then subsequently probed. For cotton, melon, and sweet potato, the overall frequency of oviposition was lower than reported in previous studies. Results from these studies showed that the greatest factor in influencing overall parasitism in laboratory experiments was the propensity of females to alight and remain to search for hosts on a particular host plant. The role of "pre-conditioning" parasitoids to be better-suited to a particular host or host plant species is discussed relative to the findings herein.

KEY-WORDS: behavior, biological control, parasitism, whiteflies, natal host plant.

Eretmocerus sp. nr. *californicus* Howard is the principal parasitoid species attacking silverleaf whitefly in California desert areas (unpublished data). Field studies conducted in the agricultural region of southeastern California known as the Imperial Valley showed that percentage parasitism by *E. sp. nr. californicus* varied greatly among plant species sampled (unpublished data). Studies were conducted to quantify and describe the host searching and ovipositional behaviors of *Eretmocerus* sp. nr. *californicus* females reared from hosts infesting sweet potato on a variety of host plant species found in the Imperial Valley. The results showed great similarity of searching behaviors when females were offered hosts on a variety of morphologically and taxonomically distinct host plant species (Headrick *et al.*,

1995, 1996). The most significant difference was the propensity of the female wasp to remain on and search for hosts on leaves upon initial introduction to the leaf surface on these different plants (Headrick *et al.*, 1995, 1996).

The objective of the present study was to repeat the behavioral experiments conducted by Headrick *et al.* (1995, 1996), but this time with females of *E. sp. nr. californicus* reared from whitefly hosts (*Bemisia argentifolii* Bellows & Perring) infesting melon (*Cucumis melo* L.), one of the plant species used in the previous studies. Host searching and related behaviors of melon-reared females were then analyzed on the same set of host plant species for frequency and duration and for host nymphal stage-related effects. Statistical comparison was conducted only among the treatment plants in this study. Non-statistical comparison was made with results from studies for *E. sp. nr. californicus* females reared from whitefly hosts infesting the glabrous host plant sweet potato (*Ipomoea batatas* L.) in order to determine if any performance-related differences could be elucidated among females reared from different host plants.

MATERIALS AND METHODS

Colonies of silverleaf whitefly and *E. sp. nr. californicus* were maintained on melon at $24^{\circ} \pm 1^{\circ} \text{C}$ and 60 % RH. with a 14:10 light/dark photoperiod. Non-infested melon plants were maintained in greenhouses at 16-30 °C and ca. 60 % RH. Whitefly colonies and parasitoid colonies were obtained as reported by Headrick *et al.* (1995).

Behaviors of *E. sp. nr. californicus* females were recorded on video tape for subsequent description and quantification as detailed in Headrick *et al.* (1995). For each trial a single female was allowed access to the surface of an excised leaf bearing a known number of whitefly host stages ranging from 16-19 per cm² on *Abutilon theophrasti* Medic., 11-33 per cm² on *C. melo*, 7-18 per cm² on *Gossypium hirsutum* L. and 25-30 per cm² on *I. batatas* placed adaxial-side down, in a glass, 10-cm diam Petri dish. The searching behavior was recorded for 7 females on *A. theophrasti* for a total of 30 min, 22 females on *C. melo* for 172 min, 16 females on *G. hirsutum* for 170 min, and 3 females on *I. batatas* for 155 min. After each trial the presence or absence of parasite eggs was verified by microscopically examining each nymph probed by a female. Video recordings then were analyzed and each behavior, in sequence, was listed for each female, and the duration in seconds of each behavior was recorded. Female behaviors were described by Headrick *et al.* (1995) and are used herein.

Behavioral data were entered into a spread-sheet software program (Lotus 123®) and collated for statistical analysis in SAS (SAS Institute 1987). Means are based on total frequencies over all trials for each plant species, unless otherwise noted; standard errors are provided throughout. Differences among means were examined by analysis of variance (ANOVA). Differences among frequencies were examined by Chi-square analysis.

RESULTS

DEPARTURE

Females were allowed to walk onto leaf surfaces to begin searching behaviors. However, females were not constrained and could leave the leaf surface at any time. The percentage of females leaving the leaf surface without displaying any searching behavior was 29 % on *A. theophrasti*, 31 % on cotton, 71 % on melon and 0 % on sweet potato.

GENERAL BEHAVIOR

Melon-reared females exhibited searching and ovipositional behaviors similar to the generalized behavioral pathway described for females raised from sweet potato plants (Headrick *et al.*, 1995). The frequency and sequence of behaviors for melon-reared females are given in figures 1-4. For example, on *A. theophrasti*, many of the behaviors were not expressed, as movement was made difficult for wasps due to the presence of glandular trichomes (Headrick *et al.*, 1996) (fig. 1). On the remaining host plants, cotton, melon, and sweet potato, the frequency of walking (W) leading to host encounters (HE) ranged from 88 to 95 % (fig. 2, 3, 4). Oblivious host encounters (OHE) occurred from 31 to 45 % of the time. The frequency of a host encounter being followed by a circling antennation event (CA) ranged from 6 to 31 %. The frequency of initial probes (P_1) following circling antennation ranged from 59 to 68 %. Repeated probing events occurred from 0 to 30 %. Probes which led to exertion of the ovipositor under the nymph ranged from 0 to 77 %. Initial probes leading to egg deposition occurred from 6 to 14 times, repeated probes leading to egg deposition occurred from 0 to 5 times.

ANTENNATION

The duration of host assessment by antennation (CA) by melon-reared females leading to abandonment (walking), initial probes and repeated probes are given in figure 5 for *A. theophrasti*, cotton, melon, and sweet potato. On *A. theophrasti* only one circling antennation event leading to an initial probe occurred during the trials and lasted 10 sec, this is consistent with the mean durations observed on the other host plant species. There were no detectable host stage-related differences in the duration of circling antennation leading to initial probes among the various host plants (F ranges 0.08-1.81, Observed Significance Level (OSL) ranges from 0.16-0.97).

Circling antennation before a repeated probe of the same host did not occur on *A. theophrasti* or melon. Circling antennation before initial probes were significantly longer than circling antennation before repeat probes only on cotton (F = 9.31, OSL = 0.0033).

PROBING

The mean durations of initial probes, repeated probes and all probes leading to oviposition or no oviposition are given in figure 6 on all host plants tested. A single probing event of a second instar nymph occurred on *A. theophrasti* lasting 13.0 sec. There were no repeated probing attempts on melon. No Significant differences between initial and repeat probe durations were detected (cotton: F = 2.23, OSL = 0.140; sweet potato: F = 0.91, OSL = 0.35). On cotton (F = 3.81, OSL = 0.06), melon (F = 0.18, OSL = 0.84), and sweet potato (F = 0.3, OSL = 0.74), no stage-related differences in probing durations leading to oviposition were detected.

OVIPOSITION

On cotton, oviposition occurred under 13 of 21 (62 %) nymphs under which ovipositor exertion occurred. On melon oviposition occurred under 6 of 6 (100 %) of the nymphs, and on sweet potato oviposition occurred under 17 of 33 (51 %) of the nymphs.

Oviposition by melon-reared females was also analyzed for frequency and host nymphal stage effects for cotton, melon and sweet potato (fig. 7a, b, c, d).

For cotton, melon, and sweet potato proportionally fewer first instar nymphs were encountered than expected by random chance based on their abundance (cotton:

Abutilon theophrasti

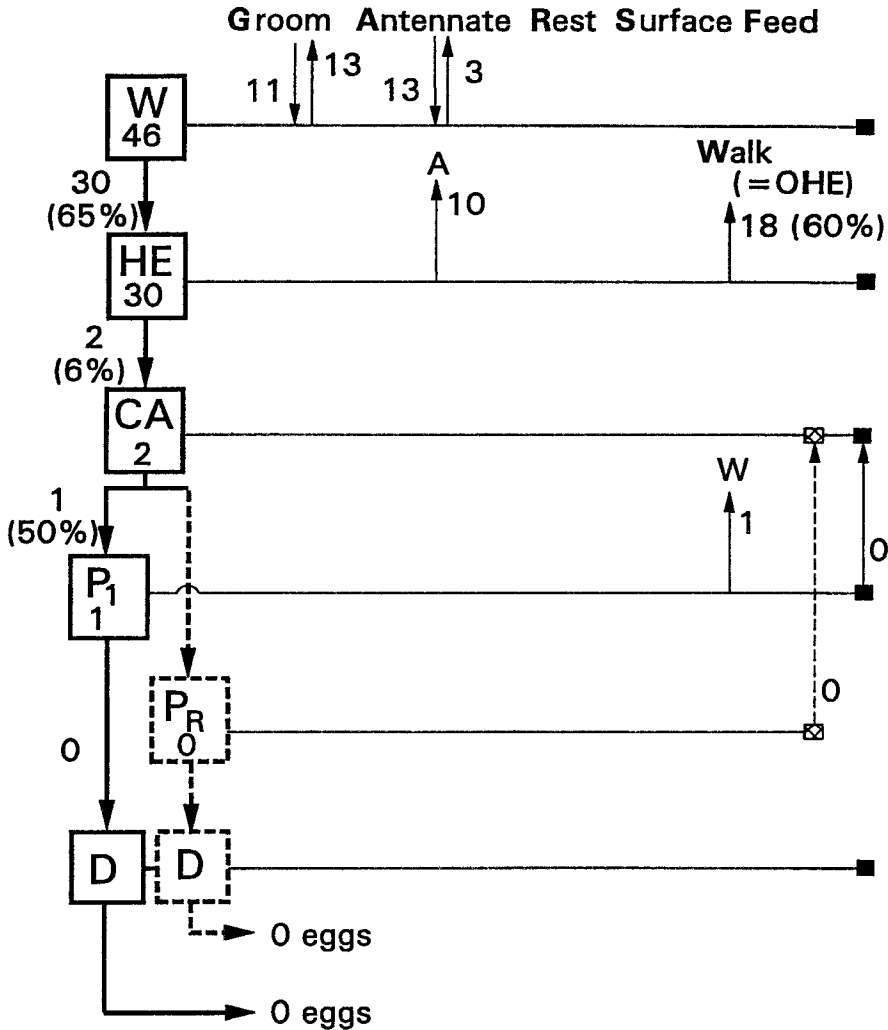


Fig. 1. Ethogram for behaviors leading to oviposition of *E. sp. nr. californicus* attacking *B. argentifolii* on *A. theophrasti*. Arrows indicate subsequent behavioral events and the associated numbers indicate the frequency of observation, summed over all trials. The main behavioral pathway begins at the top left, in bold-face, and moves down the left margin. The numbers associated with each behavior type are the frequency of observation collated over all trials. The behavioral sequences for host reassessment and repeated probes are indicated by the dashed lines and arrows. Host feeding behaviors were not included in this ethogram, and thus account for the slight differences between the summed behaviors leading into and out of a main behavioral pathway category. A-antennation, CA-circling antennation, D-disengagement, G-grooming, HF-host feeding, HE-host encounter, OHE-oblivious host encounter, P₁-initial probe, P_R-repeat probe, PVO-probing the vasiform orifice, R-resting, SF-surface feeding (= non-host feeding), W-walking, *-indicates host feeding episodes which were not considered in the frequency analysis of the general behavioral pathway.

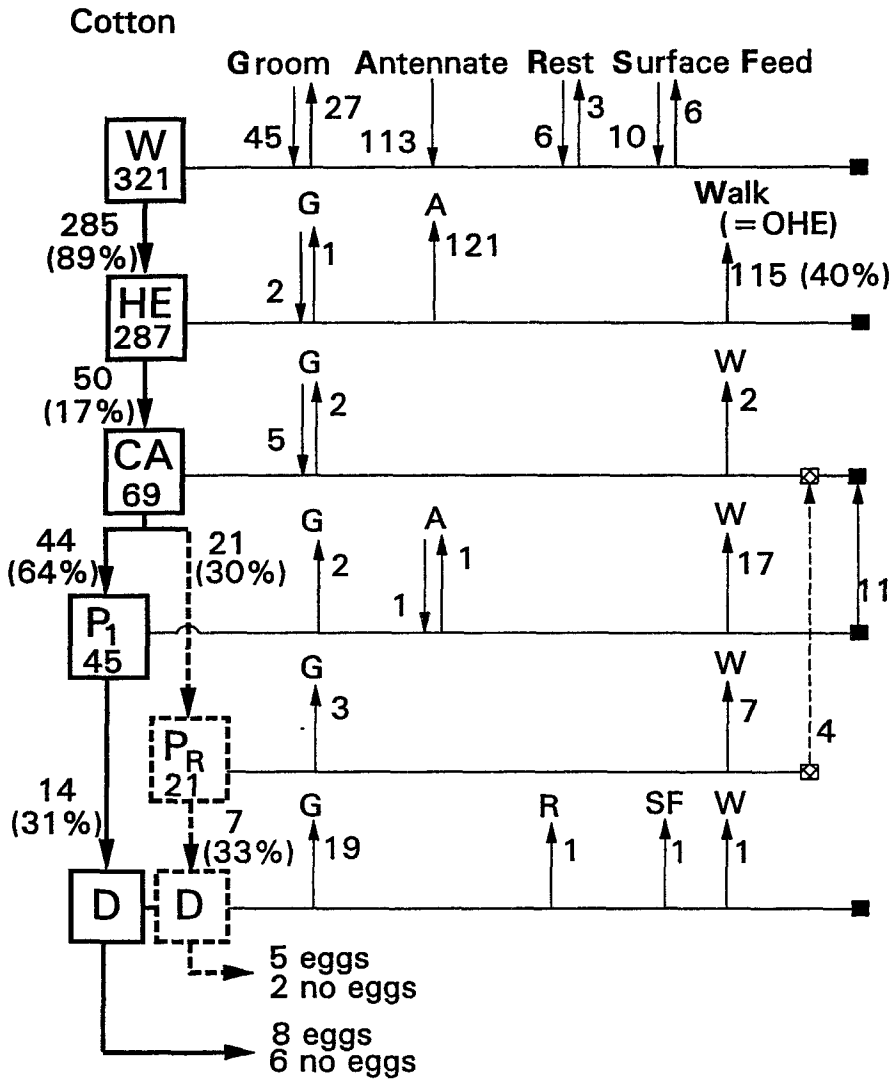


Fig. 2. Ethogram for behaviors leading to oviposition of *E. sp. nr. californicus* attacking *B. argentifoli* on cotton. Explanation and abbreviations as given for Fig. 1.

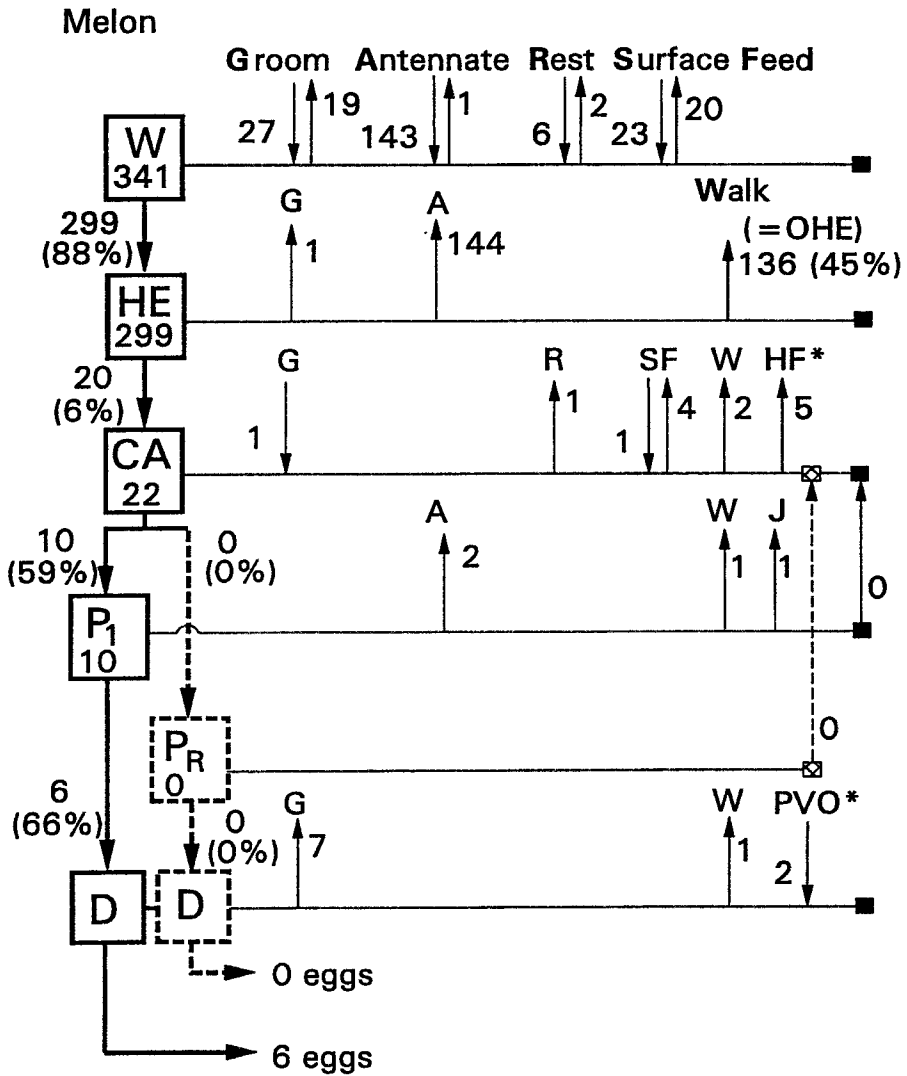


Fig. 3. Ethogram for behaviors leading to oviposition of *E. sp. nr. californicus* attacking *Bemisia argentifolii* on melon. Explanation and abbreviations as given for Fig. 1.

Sweet potato

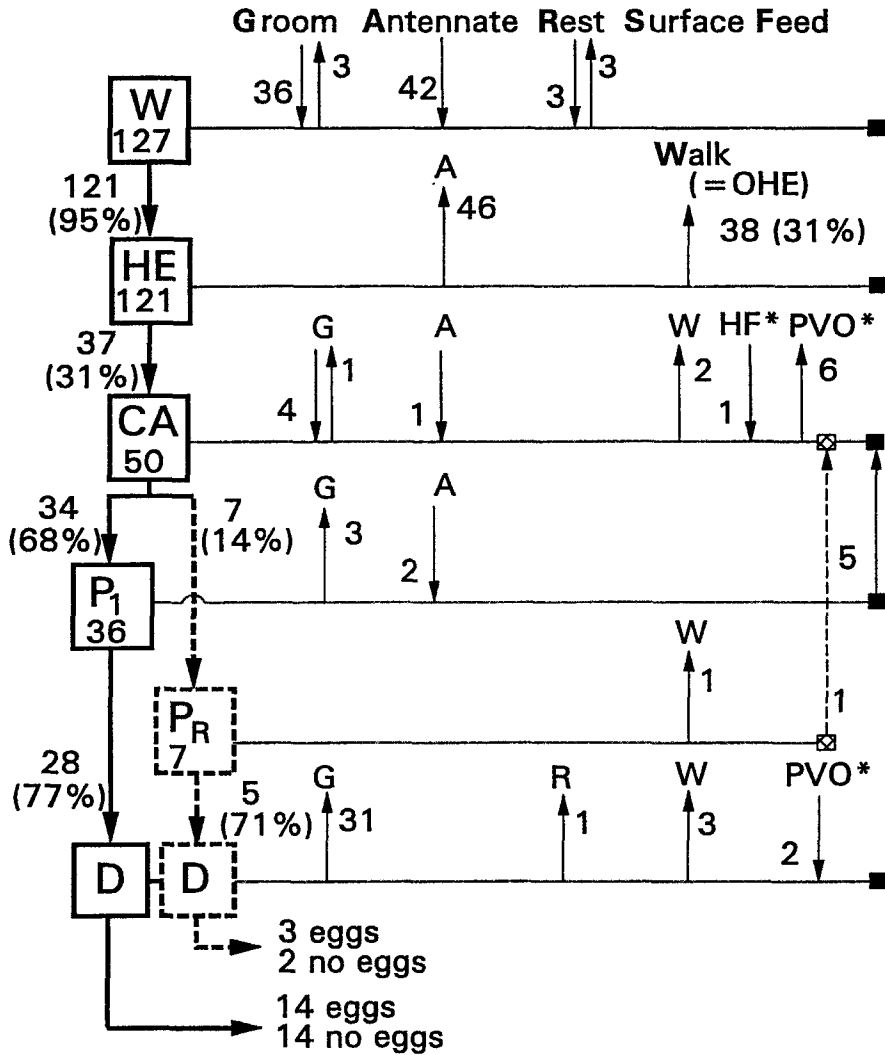


Fig. 4. Ethogram for behaviors leading to oviposition of *E. sp. nr. californicus* attacking *B. argentifolii* on sweet potato. Explanation and abbreviations as given for Fig. 1.

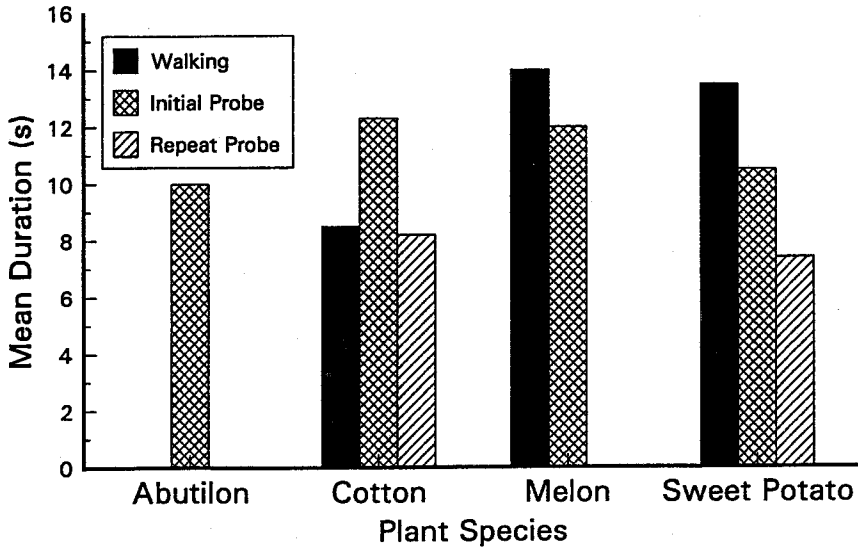


Fig. 5. Mean duration of circling antennation based on subsequent behaviors in all trials and on all nymphal stages.

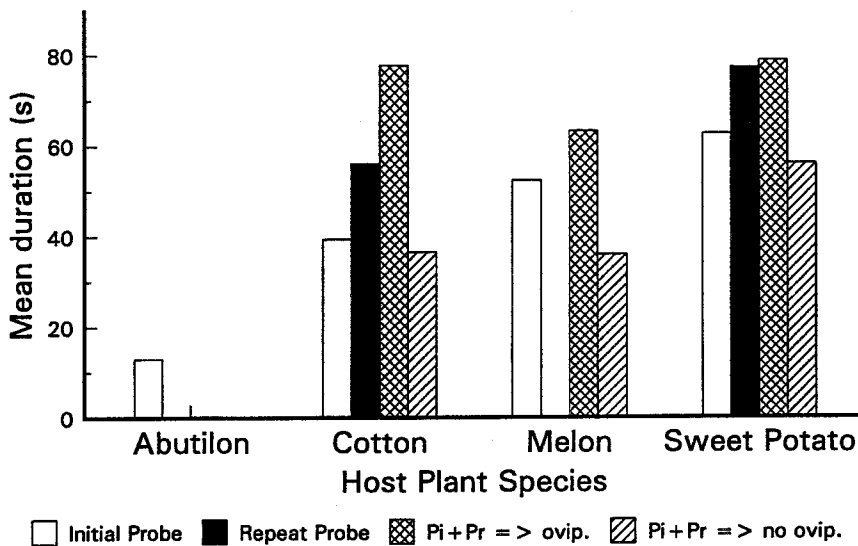


Fig. 6. Mean duration of initial and repeated probing events over all trials, and mean duration of initial and repeated probing events based on successful oviposition over all trials.

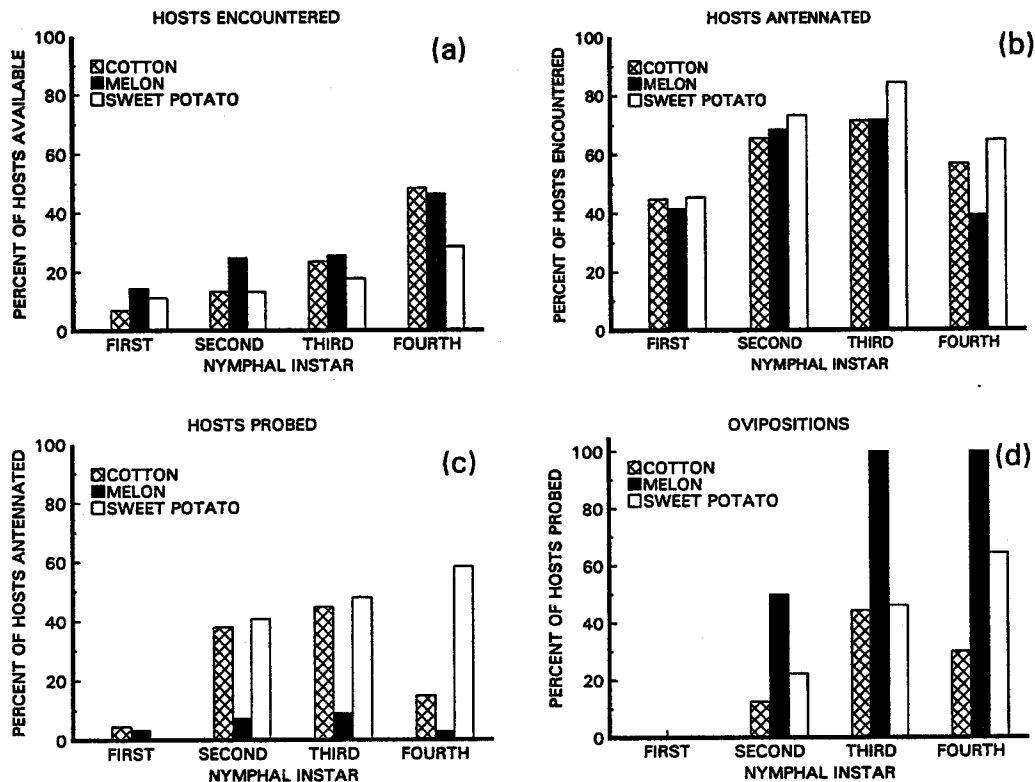


Fig. 7. Frequencies, represented as a percentage, of behavioral events leading to oviposition by nymphal instar on three host plant species: cotton, melon, and sweet potato (see text for explanation and statistical differences). (a) Of the numbers available, those which were encountered; (b) of those encountered, those which were antennated; (c) of those antennated, those which were probed; (d) of those probed, those which received an egg.

$X^2 = 231.825$, d.f. = 3, OSL < 0.001; melon: $X^2 = 75.743$, d.f. = 3, OSL < 0.001; sweet potato: $X^2 = 19.47$, d.f. = 3, OSL < 0.001). On cotton and melon, a larger proportion of fourth instar nymphs were encountered than expected (cotton: $X^2 = 105.5$, d.f. = 2, OSL < 0.001; melon: $X^2 = 30.25$, d.f. = 2, OSL < 0.001). For cotton, melon and sweet potato, a larger proportion of the second instar nymphs that were encountered were subsequently antennated than expected (cotton: $X^2 = 9.0$, d.f. = 3, OSL = 0.03; melon: $X^2 = 26.17$, d.f. = 3, OSL < 0.001; sweet potato: $X^2 = 9.72$, d.f. = 3, OSL = 0.02). For cotton, a significantly larger proportion of second instar nymphs that were antennated were subsequently probed ($X^2 = 20.07$, d.f. = 3, OSL = 0.002). On melon, there were no differences detected in the frequency among nymphal instars which were probed subsequent to antennation ($X^2 = 1.46$, d.f. = 3, OSL = 0.69). On sweet potato, no first instar nymphs were probed after antennation, and among the remaining instar nymphs there were no significant differences detected for probing ($X^2 = 2.515$, d.f. = 2, OSL = 0.113).

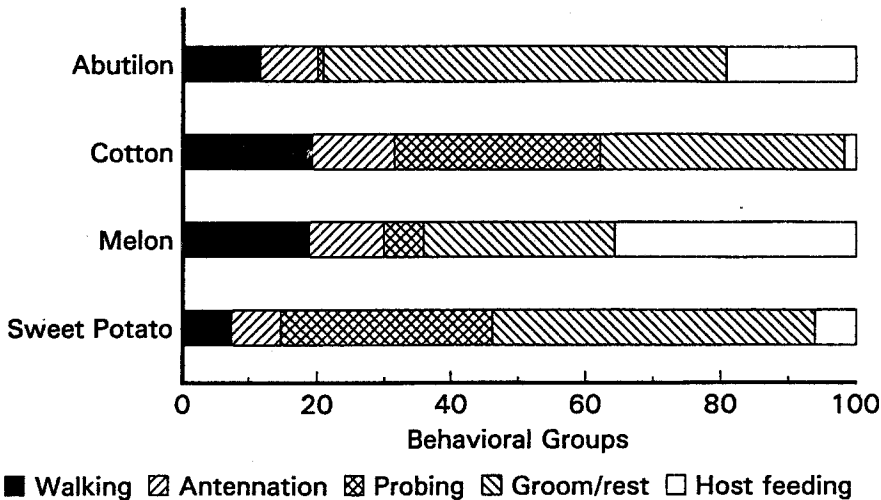


Fig. 8. Time budget of *E. sp. nr. californicus* females attacking *B. argentifolii* on summed over all trials.

Based on these data there were no detectable patterns in the frequency of oviposition among instars, with the exception that no first instar nymphs received an egg (cotton: $X^2 = 4.62$, d.f. = 3, OSL = 0.20; melon: $X^2 = 4.33$, d.f. = 3, OSL = 0.23; sweet potato: $X^2 = 3.90$, d.f. = 2, OSL = 0.14).

OVERALL TIME BUDGET

Walking ranged from 7.4 to 19.2 % of the total time on the four host plants examined (fig. 8). Antennation ranged from 7.3 to 12.25 % of the total time, probing ranged from 0.8 to 31.5 % of the total time, grooming/resting ranged from 28.5 to 60 % of the total time, and host feeding ranged from 1.79 to 35.6 % of the total time (fig. 8). Behaviors associated with host location, assessment and oviposition (walking, antennation, probing) accounted for the majority of time on cotton and melon, and about half the time spent on sweet potato. The behaviors associated with grooming and resting were the most time consuming individual activities over all plant species.

DISCUSSION

The behaviors of female *E. sp. nr. californicus* are fairly invariant in regards to the general behavioral pathway and the duration of behavioral events (Headrick *et al.*, 1995, 1996). The behavior which varies most closely with the observed percentage parasitism in the field is the propensity of a female wasp to remain and search for hosts on a particular host plant species. In general, *E. sp. nr. californicus* females did not search for hosts on plants that have leaves which were hirsute, or possessed glandular trichomes. Of the females that did remain and search for hosts, the relative frequency of ovipositions per unit

time was related closely to mechanical constraints based on the leaf surface morphology upon which the host nymph occurred (Headrick *et al.*, 1996).

The duration of circling antennation leading to abandonment was similar for all melon-reared females on cotton, melon and sweet potato and was similar to earlier studies with sweet potato-reared females (Headrick *et al.*, 1995, 1996). This indicates that the duration of the process of recognizing and evaluating a host by means of circling antennation and subsequently rejecting that host is similar irrespective of the host plant species upon which the host occurs and from which host plant the female wasp was reared. The similarity in circling antennation duration among all treatments indicates the function of assessing hosts for probing is mainly influenced by mechanical constraints of circling the host. Apparent mechanical constraints consist of the presence of leaf hairs or other obstructing structures.

The duration of probing events were similar for melon-reared females among the different host plants. Again, we find that relatively few observable differences in frequency and duration among the treatments indicates that host plant structure and natal host plant effects on female probing behavior were minimal.

Additionally, we found that where performance differences between the present study and those reported for sweet potato-reared females occurred, melon-reared females were relatively outperformed by sweet potato-reared females (*e.g.*, propensity to remain on leaf surfaces and, subsequent to detection, the frequency of antennation, probing and oviposition). These findings may have bearing on eventual augmentative biological control programs. Pre-conditioning of parasitoids for specific hosts and host plant species under insectary conditions has been suggested as a method to obtain "better-suited" biological control agents (Prokopy & Lewis, 1993). The data from the present study suggests further testing is required before the development of separate mass-production colonies of *E. sp. nr. californicus* on different host plant species is pursued as the overall performance of female wasps reared from different host plants is not substantially altered from previously reported studies.

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RÉSUMÉ

Effets de la plante hôte sur le comportement des femelles de *Eretmocerus sp. nr. californicus* obtenues à partir de *Bemisia argentifolii* élevé sur melon.

Le comportement des femelles d'*Eretmocerus sp. nr. californicus*, élevées sur *Bemisia argentifolii* Bellows & Perring sur melon, *Cucumis melo* L., a été étudié avec 4 plantes hôtes différentes (coton, melon, patate douce et *Abutilon theophrasti* Medic.). La comparaison avec des résultats publiés antérieurement concernant des femelles élevées sur des plants de patate douce, montre des différences dans les séquences comportementales précédant l'oviposition. Dans la présente étude, l'ensemble des séquences comportementales (locomotion, rencontre de l'hôte, exploration à l'aide des antennes, piqûre et oviposition) ne présente pas de différences entre plantes hôtes pour les parasitoïdes femelles élevés sur melon. L'examen de l'hôte à l'aide des antennes, qui permet l'acceptation puis la piqûre varie de 10,5 à 12,3 s entre les plantes hôtes, sans différence de durée liée au stade larvaire. La piqûre initiale et la piqûre répétée (piqûres multiples sur le même hôte au stade nymphé) durent de 52,4 à

77,3 s selon la plante, sans relation avec le stade de l'hôte. Sur coton, l'oviposition a lieu dans 62 % des nymphes, sur melon 100 % et sur patate douce 51 % des nymphes dont le parasitoïde a retiré son ovipositeur. Sur coton, melon et patate douce, moins de larves de premier stade que prévu sous une hypothèse de répartition au hasard ont été trouvées ; une plus grande proportion de larves de deuxième stade a été l'objet d'un examen antennaire et une plus grande proportion de larves de second stade a été ensuite piquée sur coton. Pour le coton, le melon et la patate douce, la fréquence totale d'oviposition était plus basse que celle notée dans des travaux antérieurs. Ces recherches montrent qu'en laboratoire, le facteur principal qui influence le parasitisme global est la faculté des femelles à se poser et rester sur une plante hôte donnée pour y rechercher un hôte. Le rôle du pré-conditionnement du parasitoïde pour une meilleure adéquation à un hôte ou à une plante hôte donnés est discuté dans le cadre des résultats obtenus dans la présente étude.

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