

**BEHAVIOR OF FEMALE *ERETMOCERUS* SP. NR. *CALIFORNICUS* HOWARD
(APHELINIDAE: HYMENOPTERA) ATTACKING *BEMISIA ARGENTIFOLII*
BELLOWS AND PERRING (ALEYRODIDAE: HOMOPTERA) ON TWO NATIVE
CALIFORNIAN WEEDS**

DAVID H. HEADRICK, THOMAS S. BELLOWS, JR., and THOMAS M. PERRING
Department of Entomology, University of California at Riverside, Riverside, California, USA 92521

Abstract

Searching and ovipositional behaviors by female *Eretmocerus* sp. nr. *californicus* Howard on *Bemisia argentifolii* Bellows and Perring infesting velvetleaf, *Abutilon theophrasti* Medic. (Malvaceae), and telegraph weed, *Heterotheca grandiflora* Nutt. (Asteraceae), were quantified. Adult female behaviors were described and quantified for *E. sp. nr. californicus* to establish a behavioral time budget analysis. Females departed from leaves of *A. theophrasti* in 83.3% of the trials, and of those that remained and searched for hosts, walking speeds averaged 0.29 mm/s. Females departed from the leaves of *H. grandiflora* in 44.4% of the trials, and those remaining readily searched for whitefly hosts with walking speeds averaging 0.26 mm/s. The duration of host assessment by antennation was related to subsequent behaviors; rejecting a host was a shorter process than accepting it for further evaluation irrespective of plant species or nymphal stage. Evidence for a behavioral preference for oviposition under early nymphal instars was documented for female *E. sp. nr. californicus* on both plant species. Oviposition efficiency in 1-h laboratory trials for nymphs on *A. theophrasti* was 30% and efficiency on *H. grandiflora* was 23%. Females spent 61.9 and 53.3% of their total time in searching, host assessment, probing, and oviposition while on *A. theophrasti* and *H. grandiflora*, respectively. The remainder of the time was spent grooming, resting, and host feeding, except host feeding on *A. theophrasti* was not observed. Implications of this study for silverleaf whitefly management through conservation and augmentation of native flora and fauna are discussed.

Résumé

Les comportements de recherche d'hôtes et de ponte ont été quantifiés chez des femelles d'*Eretmocerus* sp. près de *californicus* Howard en présence d'aleurodes *Bemisia argentifolii* Bellows et Perring infestant des plants de la fausse guimauve *Abutilon theophrasti* Medic. (Malvaceae), et de l'aster *Heterotheca grandiflora* Nutt. (Asteraceae). La description quantifiée de ces comportements a permis de faire l'analyse du budget temporel du comportement. Les femelles ont quitté les feuilles d'*A. theophrasti* dans 83,3% des expériences et celles qui sont restées et y ont cherché un hôte le faisaient en se déplaçant à 0,29 mm/s en moyenne. Les femelles ont quitté les feuilles d'*H. grandiflora* dans 44,4% des expériences et celles qui sont restées sur les plants ont recherché un aleurode hôte en se déplaçant à 0,26 mm/s. La durée de l'évaluation d'un hôte par utilisation des antennes était liée aux comportements subséquents: le rejet d'un hôte supposait un processus plus court que son acceptation en vue d'une évaluation plus approfondie, quel qu'ait été l'espèce de plante ou le stade larvaire de l'hôte. Les femelles d'*Eretmocerus* sp. près de *californicus* manifestaient une tendance évidente à pondre de préférence sous les larves de premier stade de l'homoptère, sur les deux espèces de plantes. L'efficacité à pondre sur des larves de l'homoptère au cours d'essais en laboratoire d'une durée de 1 h a été évaluée à 30% sur *A. theophrasti* et à 23% sur *H. grandiflora*. Les femelles ont passé 61,9% de leur temps à chercher, à évaluer leur hôte, à explorer et à pondre sur la fausse guimauve et 53,3% sur l'aster. Le reste du temps a été occupé au toilettage, au repos et à l'alimentation sur l'hôte (cette activité n'a pas été observée sur *A. theophrasti*). Les effets de ces résultats sur le contrôle

des populations de l'aleurode par le biais de la conservation et de l'augmentation de la flore et de la faune indigènes sont examinés.

[Traduit par la Rédaction]

Introduction

Research reported herein is part of a larger study that describes searching and ovipositional behaviors of female *Eretmocerus* sp. nr. *californicus* Howard attacking the silverleaf whitefly, *Bemisia argentifolii* Bellows and Perring, on a variety of host plants. *Eretmocerus* sp. nr. *californicus* is the principal species of parasitic Hymenoptera attacking *B. argentifolii* in the Imperial Valley of southern California. However, percentage parasitism by *E. sp. nr. californicus* varies greatly among agricultural, ornamental, and native plant species in this area (TSB, unpublished data).

The objectives of the overall study are to quantify searching and ovipositional behaviors of female *E. sp. nr. californicus* on five host plant species that represent a broad taxonomic and morphological spectrum. Studies on the extent to which the searching and oviposition behaviors of female *E. sp. nr. californicus* vary among sweet potato, melon, and cotton have been completed (Headrick et al. 1995, 1996). Herein, we present our findings of the behaviors on two native Californian weed species, *Abutilon theophrasti* (Medic.) (Malvaceae) and *Heterotheca grandiflora* Nutt. (Asteraceae). These weeds occur commonly along road cuts or other disturbed areas in the desert agroecosystems of southern California. The leaves of *A. theophrasti* are densely covered with glandular trichomes that maintain an oily droplet. The leaves of *H. grandiflora* also are densely covered with trichomes and leaf hairs, but the trichomes produce a highly viscous exudate that does not adhere to the integument of the parasitoids.

Materials and Methods

Colonies of silverleaf whitefly and *E. sp. nr. californicus* were obtained and maintained as reported by Headrick et al. (1995). Behaviors of female *E. sp. nr. californicus* were recorded on video tape for later description and quantification (Headrick et al. 1995). For each trial a single female was placed on the surface of an excised leaf bearing a known number of whitefly host stages ranging from 9.25 to 18.25 per cm² on *A. theophrasti* and from 2.0 to 4.0 per cm² on *H. grandiflora*, placed adaxial-side down, in a glass, 10-cm-diameter Petri dish. Whitefly densities were variable, in part because of the presence of glandular trichomes. Whitefly densities fell within the ranges reported for sweet potato, cotton, and melon (Headrick et al. 1995, 1996). In those studies walking speeds and other behaviors showed little variation in their duration and thus were not much affected by whitefly density per se. All trials were conducted between 1000 and 1600 hours. The searching behavior of six females on leaves of *A. theophrasti* and 18 females on leaves of *H. grandiflora* were recorded. After each trial the presence or absence of parasite eggs was verified by microscopically examining each nymph probed by a female.

Analysis of behavioral data was conducted as reported by Headrick et al. (1995, 1996). 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) with an observed significance level of 0.05. Differences among frequencies were examined by chi-square analysis with an observed significance level of 0.05.

Results

Ethograms for female *E. sp. nr. californicus* were developed from the recorded sequences. Females typically exhibited behaviors in the following order after being introduced to a leaf: walking on the leaf surface, encountering a host, assessing that host

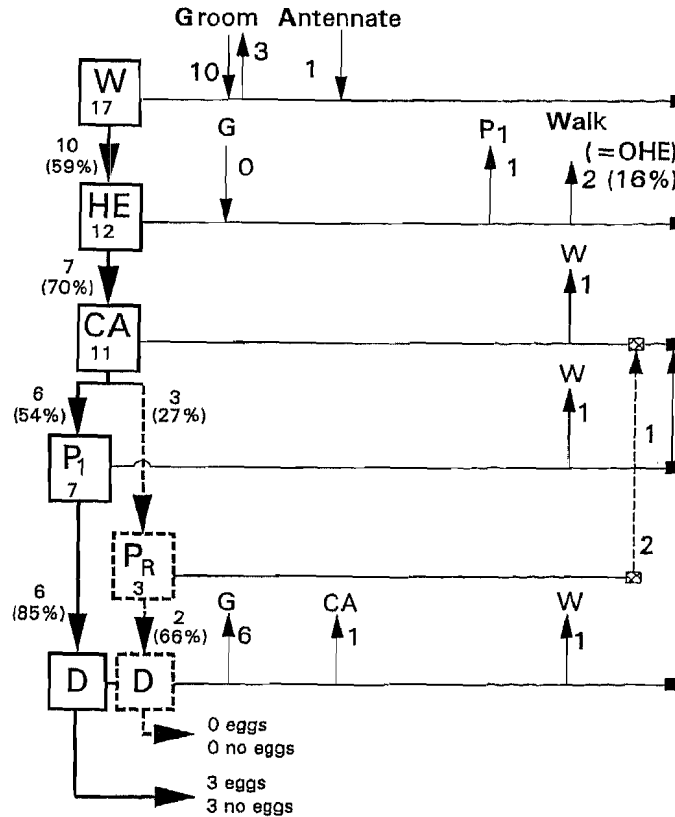


FIG. 1. Ethogram for behaviors of *Eretmocerus* sp. nr. *californicus* attacking *Bemisia argentifolii* on *Abutilon theophrasti*. Arrows indicate subsequent behavioral events and the associated numbers indicate the frequency of observation, collated over all trials. The main behavioral pathway begins at the top left and moves down the left margin. The number associated with each behavior category is the frequency of observation collated over all trials. Percentages of the total frequency are included for each step in the behavioral pathway. The behavioral sequences for host assessment, probing, and reassessment and their frequencies are indicated by the larger vertical arrows on the right. CA = circling antennation, D = disengagement, G = grooming, HE = host encounter, OHE = oblivious host encounter, P₁ = initial probe, P_R = repeat probe, W = walking.

with antennation, probing the host for oviposition or host feeding, and then sometimes repeating the process (Headrick et al. 1995). Complexity within this main behavioral pathway occurred through intervening behaviors such as grooming, resting, or resumption of walking. Within the general pathway, frequencies of behavioral sequences were recorded (Figs. 1 and 2). The main behavioral pathway is shown from top to bottom on the left. Arrows are associated with the horizontal lines to the right of each of the main behavioral pathway components and indicate the frequencies of behaviors that led to or were followed by the behavior on the left. For example in Figure 1, walking (W) led to grooming (G) three times and grooming was followed by walking 10 times, disengagement (D) was followed by walking once, and antennation (A) was followed by walking once. Continuing down the main pathway on the left, walking on leaves of *A. theophrasti* led to host encounters (HE) 10 (59%) times. Host encounters led to arrestment and subsequent circling antennation (CA) seven (70%) times, and so on. If an initial probe did not lead to exertion of the ovipositor under a host nymph, reassessment of the host occurred (Fig. 1, far right, broken upward vertical arrow). Repeated probes (P_R) are indicated by broken lines. Exsertion of the

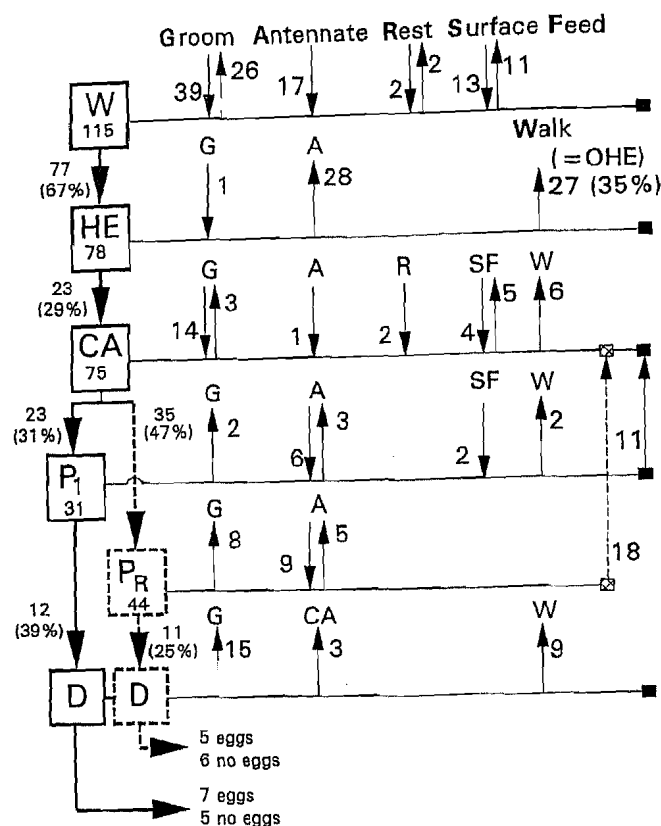


FIG. 2. Ethogram for behaviors of *Eretmocerus* sp. nr. *californicus* attacking *Bemisia argentifolii* on *Heterotheca grandiflora*. Arrows indicate subsequent behavioral events and numbers indicate the frequency of observation collated over all trials. The main behavioral pathway begins at the top left and moves down the left margin. The behavioral loops for host assessment, probing, and reassessment and their frequencies are indicated by the broken arrows. A = antennation, CA = circling antennation, D = disengagement, G = grooming, HE = host encounter, OHE = oblivious host encounter, P₁ = initial probe, P_R = repeat probe, R = resting, SF = surface feeding (= non-host feeding), W = walking.

ovipositor under a host nymph did not always result in egg deposition. After disengagement (D), the host was abandoned and not revisited by the same female if searching continued.

All behaviors were analyzed to determine which of three factors [(1) host nymphal stage; (2) preceding or subsequent behaviors; and (3) host plant species] had any impact on their frequency or duration.

Walking Speed. We found that 83% of the females left the surfaces of leaves of *A. theophrasti* without exhibiting any searching or became mired in the trichome resins: 44% of the females abandoned the leaves of *H. grandiflora* without any searching. Walking speeds by female *E. sp. nr. californicus* on *A. theophrasti* were, on average, 0.29 mm/s, whereas on *H. grandiflora* they were, on average, 0.26 mm/s.

Host Encounters. Three of the six females recorded in the trials on *A. theophrasti* were able to move about and search on leaves that either had begun to senesce and the resins had dried, or where the adult whiteflies were numerous enough that the plant resins had been coated with their waxes. In these three trials, 17 searching episodes led to encountering 12 host nymphs (Fig. 1). Females moved away from encountered hosts without displaying any behaviors (OHE) two (16%) times. Arrestment by a female was indicated by antennation of

TABLE 1. Mean duration in seconds [mean \pm SE (*n* and range)] of antennation and probing behaviors of female *Eretmocerus* sp. nr. *californicus* females attacking *Bemisia argentifolii* on *Abutilon theophrasti* and *Heterotheca grandiflora*

Behavior	Plant species	
	<i>A. theophrasti</i>	<i>H. grandiflora</i>
Circling antennation		
Followed by:		
Abandonment	3.5 (1)	17.6 \pm 7.0 (6, 1.0–46.0)
Initial probe	15.8 \pm 2.6 (6, 10.0–29.0)	16.5 \pm 1.4 (23, 6.0–38.0)
Repeat probe	9.3 (1)	11.4 \pm 1.1 (35, 3.0–37.0)
Antennation without circling		
Followed by:		
Abandonment	1.0 (1)	9.5 \pm 2.1 (12, 1.0–26.0)
Initial probe	—	6.7 \pm 1.8 (6, 2.0–14.0)
Repeat probe	—	7.4 \pm 0.5 (9, 6.0–11.0)
Probing		
Total duration:		
Initial probe	120.8 \pm 26.45 (7, 17.0–213.0)	70.9 \pm 17.6 (31, 4.0–507.0)
Repeat probe	111.3 \pm 42.2 (3, 27.0–157.0)	43.4 \pm 11.7 (44, 3.0–339.0)
Leading to oviposition:		
Initial probe	132.3 \pm 12.1 (3, 116.0–156.0)	140.7 \pm 14.7 (7, 75.0–190.0)
Repeat probe	—	228.0 \pm 46.1 (5, 114.0–339.0)
Followed by no oviposition:		
Initial probe	112.2 \pm 48.1 (4, 17.0–213.0)	51.3 \pm 20.6 (24, 4.0–507.0)
Repeat probe	—	19.8 \pm 4.1 (39, 3.0–152.0)

the host which involved continued drumming of the apices of her antennae asynchronously on the dorsum of the host. Antennation either was followed by abandonment (walking) of the host or continued assessment of the host by antennation in a pattern referred to as circling antennation (Fig. 1, CA) (Headrick et al. 1995). On *A. theophrasti*, circling antennation was impaired by the presence of glandular trichomes around the nymphs and the accumulated resins on the female wasps. The frequency of host encounters leading to circling antennation on *A. theophrasti* was seven of 12 (70%).

On *H. grandiflora*, the movements of females were not affected by the glandular trichomes, as the resins were more viscous than on *A. theophrasti* and did not adhere to their integument. Searching led to host encounters 77 (67%) of 115 times (Fig. 2). We perceived that females often missed recognizing host nymphs because of the difficulty in maneuvering around the numerous leaf hairs. On *H. grandiflora*, continued searching without any observable arrestment after a host encounter, or an oblivious host encounter, occurred 27 (35%) times (Fig. 2, OHE). The frequency of host encounters leading to circling antennation was 23 of 78 (29%). The frequency of host encounters was not influenced by the host nymphal stages, or preceding or subsequent behaviors.

Antennation. Durations of circling antennation on *A. theophrasti* (Table 1) led to initial probes only on second-instar (*n* = 2) and fourth-instar (*n* = 4) nymphs. Antennation without circling on *A. theophrasti* led to abandonment only once (Table 1), and did not precede any probing events.

There were no detectable differences in circling antennation leading to abandonment or initial probes on *H. grandiflora* (Table 1) ($F = 0.07$, $OSL = 0.78$). After the initial probe, reassessment of the host by circling antennation was significantly shorter than the mean duration of the circling antennation leading to an initial probe (Table 1) ($F = 8.4$, $OSL = 0.005$).

The differences in non-circling antennation durations leading to abandonment or initial probes on *H. grandiflora* were not significant ($F = 0.8$, $OSL = 0.4$). Antennation of the host without circling leading to repeat probes was not significantly shorter than antennation without circling leading to an initial probe (Table 1) ($F = 0.25$, $OSL = 0.62$). There were no host stage-related differences in the means calculated above.

Probing. Subsequent to probing, females most often groomed ($n = 6$ on *A. theophrasti*, $n = 15$ on *H. grandiflora*) or walked away from the host nymph ($n = 1$ on *A. theophrasti*, $n = 9$ on *H. grandiflora*). If a suitable gap between the host whitefly nymph and leaf surface was not found during the initial probe, the female then either abandoned the host ($n = 1$ on *A. theophrasti*, $n = 2$ on *H. grandiflora*) or returned to antennation of the host's margin ($n = 1$ on *A. theophrasti*, $n = 11$ on *H. grandiflora*). If circling antennation of the same host took place after an initial probe it always was following by another probing attempt (Figs. 1 and 2, vertical line leading from CA to P_R), either on the same side as the initial probe or on the side opposite. Successful exertion of the ovipositor under a host nymph on *A. theophrasti* occurred on the initial probe six times; and exertion after repeated probing attempts occurred twice; while on *H. grandiflora* the occurrences were 12 and 11, respectively.

The means of initial and repeat probes were not significantly different in duration on *A. theophrasti* ($F = 0.04$, $OSL = 0.85$) or *H. grandiflora* ($F = 1.82$, $OSL = 0.18$) (Table 1). Initial probes that led to oviposition were not significantly different among stages.

Oviposition. Probes that resulted in full exertion of the ovipositor beneath the host did not indicate successful oviposition. Only three of the eight (37%) nymphs under which ovipositor exertion occurred on *A. theophrasti* received an egg. Oviposition occurred under 12 of 23 (52%) nymphs on *H. grandiflora*.

Three eggs were laid under nymphs on *A. theophrasti* by a single female, two eggs under second-instar nymphs and one under a fourth-instar nymph. A total of 12 eggs was laid by five of the 18 females used in all trials on *H. grandiflora*. The maximum number of eggs laid by a female was three.

On *A. theophrasti*, first-, second-, third-, and fourth-instar nymphs represented 46.5, 20, 5.1, and 28.4%, respectively, of the stages present in all trials. Variation between the frequency of nymphal stages available and the frequency of them being encountered by a female searching (Fig. 3a) were not highly significant ($\chi^2 = 0.37$, $df = 3$, $OSL = 0.95$). The average proportion of stages encountered on *A. theophrasti* was 2.3%. There were no stage-related differences between the frequency of host stage encountered and the frequency of that stage being antennated (mean = 83.3%, $\chi^2 = 1.85$, $df = 1$, $OSL = 0.17$) (Fig. 3b). Of the nymphs antennated, all second instars were subsequently probed, and probing under nymphs antennated averaged 70% (Fig. 3c). Finally, of nymphs probed with the ovipositor, there was a significantly lower frequency of fourth instars receiving an egg ($\chi^2 = 3.29$, $df = 1$, $OSL = 0.07$) (Fig. 3d).

First-, second-, third-, and fourth-instar nymphs represented 25.6, 27.2, 20.7, and 26.5%, respectively, of the stages present in all trials on *H. grandiflora*. There were significantly fewer first-instar nymphs encountered by searching females ($\chi^2 = 22.8$, $df = 3$, $OSL = 0.00004$); the average proportion of stages encountered on *H. grandiflora* was 24.7% (Fig. 4a). Of the stages encountered, there were no significant differences in those that were subsequently antennated ($\chi^2 = 8.49$, $df = 3$, $OSL = 0.037$) (mean = 77.5%) (Fig. 4b). A higher proportion of third-instar nymphs was probed following antennation than other instars ($\chi^2 = 5.4$, $df = 2$, $OSL = 0.067$) (Fig. 4c). Of the nymphs probed with the ovipositor,

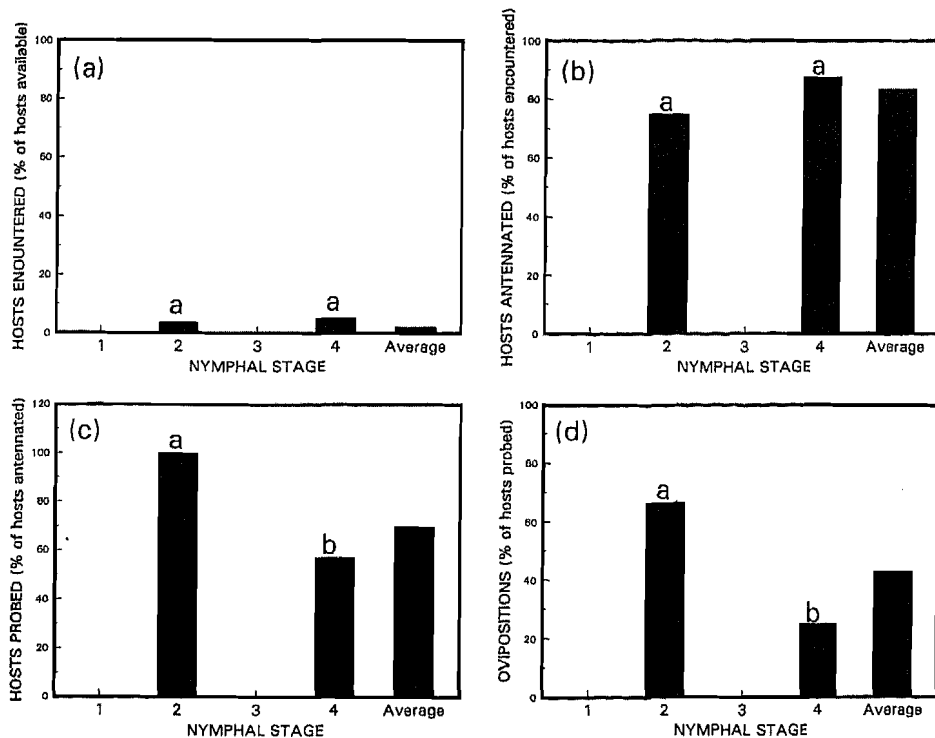


FIG. 3. Frequencies, represented as a percentage, of behavioral events leading to oviposition by nymphal instars on *Abutilon theophrasti*, columns in each figure with different letters differed in frequency with an OSL ≤ 0.05 ; weighted averages are included. (a) Of the numbers available, those that were encountered; (b) of those encountered, those that were antennated; (c) of those antennated, those that were probed; (d) of those probed, those that received an egg.

second- and fourth-instar nymphs received eggs with significantly less frequency than third-instar nymphs (mean = 37.5%, $\chi^2 = 8.69$, $df = 2$, OSL = 0.013) (Fig. 4d).

Feeding, Grooming, Resting. Feeding was divided into two categories, host feeding and surface feeding, as described by Headrick et al. (1995). Surface feeding events were not observed for females on *A. theophrasti*, but were, on average, 83.7 ± 38.3 s ($n = 37$, range 5.0–1391.0 s) on *H. grandiflora*.

Host feeding was not observed on *A. theophrasti*. Two of 18 females host fed on nymphs on *H. grandiflora*. These events took, on average, 412.6 ± 195.8 s ($n = 5$, range = 1.0–893.0 s). One female fed on a second-instar nymph for 321 s and the other female fed only on fourth-instar nymphs ($n = 4$), ranging from 1.0 to 893 s.

The mean duration of grooming for all trials on *A. theophrasti* was 97.67 ± 36.87 s ($n = 15$, range = 2.0–530.0 s). Grooming episodes on *H. grandiflora* lasted, on average, 38.1 ± 4.6 s ($n = 76$, range = 1.0–234.0 s). Resting events were not observed for females on *A. theophrasti*, but, on average, lasted 73.0 ± 15.9 s (range = 32.0–143.0 s) on *H. grandiflora*.

Overall Time Budget. Walking accounted for 27.7% of the time spent on *A. theophrasti* and 23.1% of the time spent on *H. grandiflora* (Fig. 5). Antennation behaviors comprised little of the total time spent on both plant species. Probing behaviors were relatively long, taking 30.7% of the total time spent on *A. theophrasti* and 21.4% on *H. grandiflora*. Host

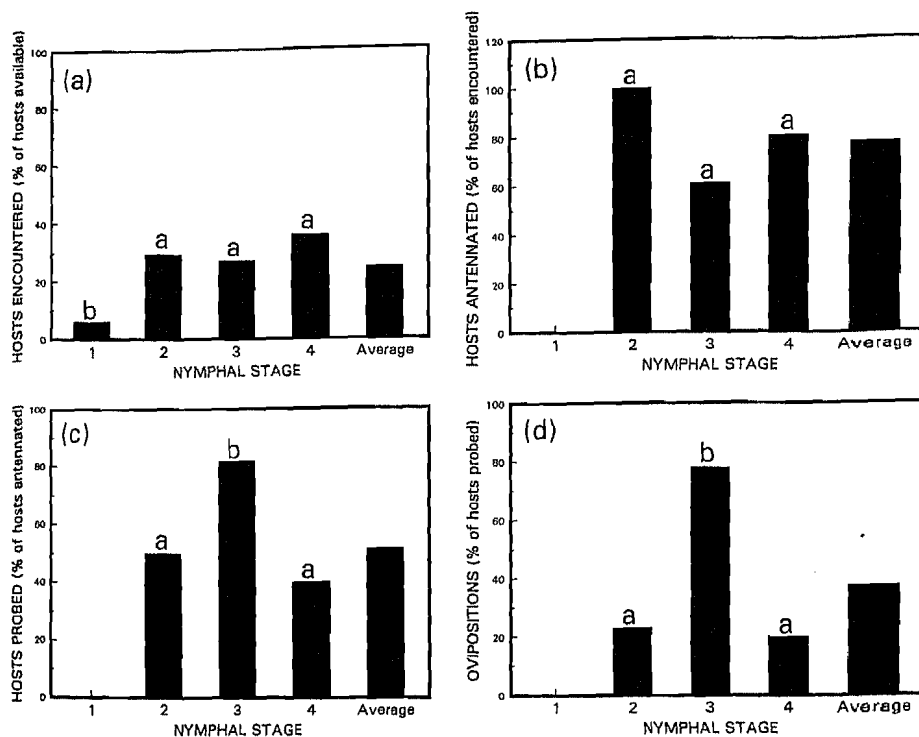


FIG. 4. Frequencies, represented as a percentage, of behavioral events leading to oviposition by nymphal instars on *Heterotheca grandiflora*, columns in each figure with different letters differed in frequency with an OSL ≤ 0.05 ; weighted averages are included. (a) Of the numbers available, those that were antennated; (b) of those encountered, those that were antennated; (c) of those antennated, those that were probed; (d) of those probed, those that received an egg.

feeding occurred only on *H. grandiflora* and accounted for 13.8% of the total time. Grooming was the most time-consuming behavior and combined with resting accounted for 38.1% of the total time on *A. theophrasti*, and 33% of the total time on *H. grandiflora* (Fig. 5).

Discussion

Various structures on host plants can impact the searching efficiency of aphelinid parasitoids by slowing or inhibiting their movements (Hua et al. 1987; Gerling 1990). Walking speeds for *E. sp. nr. californicus* on leaves of *A. theophrasti* and *H. grandiflora* were similar to walking speeds of 0.33 mm/s on melon leaves but were slower than speeds of 0.5 and 1.3 mm/s observed on leaves of cotton and sweet potato (Headrick et al. 1995). Walking speeds for *Encarsia formosa* Gahan on similarly glabrous leaves of cucumber and sweet pepper were ca. 0.8 mm/s (van Lenteren et al. 1976; van Lenteren and de Ponti 1990). We observed that searching behaviors of the female wasps, including walking and antennation, were hampered by the thick, sticky resins exuded from the glandular trichomes present on *A. theophrasti*, and on *H. grandiflora* the movements of the wasps were impaired by the numerous leaf hairs and trichomes.

We found that grooming was commonly the initial behavior for females introduced to leaves bearing hosts and was unlike that observed on leaves of sweet potato on which walking was commenced immediately upon introduction to the leaf surface (Headrick et al. 1995). During searching on *A. theophrasti* and *H. grandiflora*, females were observed to walk over



FIG. 5. Time budget analysis of female *Eretmocerus* sp. nr. *californicus* attacking hosts on *Abutilon theophrasti* and *Heterothecha grandiflora* collated over all trials.

at least some host nymphs without displaying any observable arrestment or recognition behaviors, a behavior termed "oblivious host encounters" by Headrick et al. (1995). Host recognition by females searching on these plant species was obviously impaired by the plant hairs and accumulated debris on their antennae. Females were observed to stop and groom next to or on top of a nymph and then move on without displaying recognition behaviors.

Data from the silverleaf whitefly survey in the Imperial Valley in southeastern California show that percentage parasitism on *A. theophrasti* can be low or non-existent (TSB, unpublished data). Percentage parasitism for *E. sp. nr. californicus* attacking nymphs in laboratory trials on *A. theophrasti* was 30%. Although this appears to be high when compared with field survey data, >80% of the females in laboratory trials abandoned the leaves or became coated with the resins and subsequently died. We suggest that the presence of numerous hosts may be required to, first, elicit searching behaviors in females on this plant species and, second, develop an area on the leaf in which the trichomes have been disturbed by adult whitefly activities that then can allow for female parasite searching and oviposition.

We also noted that 44.4% of the females introduced onto leaves of *H. grandiflora* for the behavioral trials left without displaying any searching behavior, whereas on glabrous-leaved plant species such as cotton and sweet potato, 77 and 100% of the females remained on the leaves, respectively (Headrick et al. 1995, 1996). This again may be indicative of the field situation, where females are avoiding plants with leaves that bear numerous hairs or glandular trichomes. However, if searching behavior is elicited on the hirsute-leaved plant species, possibly as a result of high host densities, oviposition efficiency may be enhanced by the relative ease of ovipositor exertion under the bodies of nymphs on these leaves (Headrick et al. 1996).

The results described in Figures 3 and 4 are similar to those reported for female *E. sp. nr. californicus* attacking host nymphs on sweet potato, cotton, and melon (Headrick et al. 1995, 1996) and provides further evidence for a behavioral preference for oviposition

under earlier instars. On *A. theophrasti*, females encountered only second- and fourth-instar nymphs during searching, but with equal frequency, and arrested on these stages with approximately the same relative frequency. However, females did discriminate among stages when probing with the ovipositor, probing fourth-instar nymphs much less frequently than the other stages. Females encountered first-instar nymphs on leaves of *H. grandiflora* with less frequency than expected. Of the nymphal stages encountered, females arrested and antennated them with the same relative frequency. Third-instar nymphs were subsequently probed with a slightly higher frequency than expected. Females also oviposited eggs under third-instar nymphs more frequently than under the remaining stages. Again, as noted for the other plant species (Headrick et al. 1995, 1996), females did not attempt to probe any previously assessed host nymph on either plant species and no superparasitism was noted on either weed species.

No host feeding took place on *A. theophrasti* and only two events on *H. grandiflora* were observed. The low frequency of host feeding on these plants was similar to that observed on melon, a plant with similarly hirsute leaves, and contrasts with the high frequency and duration of host feeding events on cotton and sweet potato (Headrick et al. 1995, 1996). As reported for females on sweet potato, cotton, and melon (Headrick et al. 1995, 1996), host searching and oviposition occurred directly before and after host feeding, and no host was observed to be used for both oviposition and host feeding which is consistent with findings for other aphelinids attacking Aleyrodidae (cf. Nell et al. 1976; van Lenteren et al. 1980; Gerling 1990).

The results of the silverleaf whitefly survey (TSB, unpublished data) indicate great variation in the distribution, abundance, and percentage parasitism of extant species of natural enemies among the plant species examined. Our results show that morphological and physiological features of the host plant can affect parasitoid foraging and percentage parasitism. This impinges on two aspects of classical biological control, augmentation and conservation. Conservation and augmentation of native flora have been proposed for silverleaf whitefly management in the Imperial Valley as a means of providing a resource of extant natural enemies for nearby or adjacent agricultural areas. Conservation has been proposed in terms of retaining "good" weed species while removing "bad" weed species. In this case, good and bad refer to the percentage parasitism of whiteflies associated with a particular plant species. Augmentation of "good" weed species has been proposed as a means of fortifying agricultural areas with larger numbers of natural enemies by having intensive plantings of such species or manipulating the environment in their favor. The selection criterion for such programs should require corroborative research in the field and laboratory to determine what features of the plant species facilitate natural enemy searching and oviposition.

Acknowledgments

We thank C. Meisenbacher, K. Campbell, and C. Farrar for technical support and colony maintenance. We also thank J.C. van Lenteren for helpful discussions and review of early drafts of the manuscript, and C. Meisenbacher for review of early drafts of the manuscript. This research was supported in part by UC/IPM Grant No. 93BC021, awarded to TSB and TMP.

References

- Gerling, D. 1990. Natural enemies of whiteflies: Predators and parasitoids. pp. 147–185 in Gerling, D. (Ed.), *Whiteflies: Their Bionomics, Pest Status and Management*. Intercept, UK.
- Headrick, D.H., T.S. Bellows, and T.M. Perring. 1995. Female behavior and resource allocation by *Eretmocerus* sp. nr. *californicus* (Hymenoptera: Aphelinidae) on *Bemisia argentifolii* (Homoptera: Aleyrodidae) on sweet potato, *Ipomoea batatas* (Convolvulaceae). *Environmental Entomology* 23: 412–422.

- 1996. Female behavior and resource allocation by *Eretmocerus* sp. nr. *californicus* (Hymenoptera: Aphelinidae) attacking *Bemisia argentifolii* (Homoptera: Aleyrodidae) on cotton, *Gossypium hirsutum* (Malvaceae) & melon, *Cucumis melo* (Cucurbitaceae). *Biological Control* **4**: 64–75.
- Hua, Li Zhao, F. Lammes, J.C. van Lenteren, P.W.T. Huismann, A. van Vianen, and O.M.B. de Ponti. 1987. The parasite–host relationship between *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) and *Trialeurodes vaporariorum* (Westwood) (Homoptera: Aleyrodidae). XXV. Influence of leaf structure on the search activity of *Encarsia formosa*. *Journal of Applied Entomology* **104**: 297–304.
- Nell, H.W., L.A. Sevenster-van der Lelie, J. Woets, and J.C. van Lenteren. 1976. The parasite–host relationship between *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) and *Trialeurodes vaporariorum* (Westwood) (Homoptera: Aleyrodidae). II. Selection of host stages for oviposition and feeding by the parasite. *Zeitschrift für angewandte Entomologie* **81**: 372–376.
- van Lenteren, J.C., H.W. Nell, L.A. Sevenster-van der Lelie, and J. Woets. 1976. The parasite–host relationship between *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) and *Trialeurodes vaporariorum* (Westwood) (Homoptera: Aleyrodidae). I. Host finding by the parasite. *Entomologia Experimentalis et Applicata* **20**: 123–130.
- 1980. The parasite–host relationship between *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) and *Trialeurodes vaporariorum* (Westwood) (Homoptera: Aleyrodidae). IV. Oviposition behavior of the parasite, with aspects of host-selection, host discrimination and host feeding. *Zeitschrift für angewandte Entomologie* **89**: 442–454.
- van Lenteren, J.C., and O.M.B. de Ponti. 1990. Plant-leaf morphology, host plant resistance and biological control. *Symposia Biologica Hungarica* **39**: 365–386.