

Selection of *Bemisia* nymphal stages for oviposition or feeding, and host-handling times of arrhenotokous and thelytokous *Eretmocerus mundus* and arrhenotokous *E. eremicus*

Mohammad Javad ARDEH^{1,2,*}, Peter W. de JONG¹ and Joop C. van LENTEREN¹

¹Laboratory of Entomology, Wageningen University, P.O. Box 8031, 6700 EH Wageningen, The Netherlands; ²Plant Pests and Diseases Research Institute, P.O. Box 19395-1454, Tehran, Iran

* Author for correspondence; e-mail: mohammad.javadardeh@wur.nl

Received 7 May 2004; accepted in revised form 8 September 2004

Abstract. Host-handling behavior is an important aspect of parasitoid foraging behavior. When a parasitoid encounters a potential host, the handling behavior starts with the evaluation of the host and continues if the host has been judged acceptable. Host handling is usually terminated after egg laying or host feeding and host marking. Host-handling behavior of an arrhenotokous population of two *Eretmocerus* species, *E. mundus* Mercet and *E. eremicus* Rose and Zolnerowich, along with a thelytokous population of *E. mundus* were compared under laboratory conditions. Several elements of host-handling behavior, including encountering, ascending, turning on host, descending, preening, egg laying, and host feeding were recorded. There were no correlations among the durations of these phases across parasitoid populations/species or host nymphal instars. Duration of different phases of host-handling behavior showed only slight and sometimes significant differences between different *Eretmocerus* populations/species. The actual laying of the egg had the longest duration of all host-handling behaviors, and was longer on third nymphal instars than on younger ones. Females of the three populations/species accepted the first three nymphal stages either for egg laying or for host feeding. Females spent a lot of time to make wounds in the host when preparing for host feeding, and eventually killed the host. The implications of these findings for the use of the different *Eretmocerus* populations/species in biological control are discussed.

Key words: aphelinidae, *Bemisia tabaci*, biological control, foraging behavior, host handling, host feeding, Hymenoptera

Introduction

Whiteflies are key pests worldwide (van Lenteren and Noldus, 1990; Gerling and Mayer, 1995). They cause direct feeding damage, vector a number of devastating plant viruses, reduce the quality of the harvested

product as a result of the excretion of honeydew, and can be the source of various other problems (Drost et al., 1998). Control of whiteflies with chemical pesticides is often problematic because of the wide occurrence of resistance (e.g., Palumbo et al., 2001). During the past decades, much research was directed at finding efficient natural enemies of whiteflies (for overviews, see Gerling, 1990; Gerling and Mayer, 1995; Gerling et al., 2001). To date, several species of parasitoids are used with great success to control whitefly in large commercial greenhouses (van Lenteren, 2000). The most efficient species belong to the aphelinid genera *Encarsia*, *Eretmocerus* and the Platygasterid genus *Amitus* (van Lenteren et al., 1997; Drost et al., 1999, 2000; Manzano et al., 2000, 2002; de Vis et al., 2003; Qiu et al., 2004).

Gerling et al. (2001) list 34 species of *Encarsia*, 12 species of *Eretmocerus*, two species of *Amitus*, and one species each of *Signiphora* and *Methycus* as parasitoids of *Bemisia tabaci* (Gennadius) (Hom; Aleyrodidae), which is the most serious whitefly pest of vegetable, ornamental, and agronomic crops throughout the world (Gerling, 1990; Gerling and Mayer, 1995). Gerling et al. (2001) conclude that: "with the exception of *En. formosa* Gahan (Hym.; Aphelinidae). . . and despite the frequent use of *Encarsia* species, data on their biological and taxonomic characteristics remain deficient even for commonly used species." One of these genera, *Eretmocerus*, contains two currently important commercial species: *E. eremicus* Rose and Zolnerowich (Hym; Aphelinidae) and *E. mundus* Mercet (Hym; Aphelinidae). *E. eremicus* is a native to the United States (Rose and Zolnerowich, 1997) and is an effective biological control agent of *B. tabaci* on poinsettia (Hoddle and Driesche, 1999). *E. mundus* has been recorded from many parts of the Mediterranean basin (Mound and Halsey, 1978) and is considered the most important whitefly control agent in the plastic greenhouses in southern Spain (Rodriguez et al., 1994). The two *Eretmocerus* species that are now commercially used are arrhenotokous (bisexual). Interestingly, a population of *E. mundus* has been found in Australia, which is thelytokous (asexual) (de Barro et al., 2000). As only females are effective in biological control, thelytokous reproduction can boost the effectiveness of a parasitoid in the form of lower production costs, easier establishment and quicker population growth (Stouthamer, 1993). Therefore, thelytokous *E. mundus* are considered better candidates for biological control of *B. tabaci* than arrhenotokous forms, particularly in the dry tropical regions where establishment is difficult (de Barro et al., 2000).

To develop a successful biological control program, knowledge of the foraging behavior is fundamental (Lewis et al., 1990; Godfray, 1994). During foraging, a parasitoid has to be able to find and accept a suitable

host in order to achieve reproductive success. When a parasitoid encounters a potential host, the handling behavior starts with evaluation of the host (van Lenteren et al., 1976). Host evaluation may include several steps such as antennation, probing, and drumming (van Lenteren et al., 1980; Higuchi and Suzuki, 1996; Headrick et al., 1996). In order to select a host, parasitoid females may use chemical cues or physical features of the host such as size, shape and texture (van Driesche and Bellows, 1996). Host selection is influenced by both external and internal factors, e.g., the developmental stages of the host (Vinson, 1998) and egg load of the parasitoid (Casas et al., 2000). In addition to using hosts for oviposition, females of synovigenic species, where eggs develop during the adult life of the parasitoid, often use hosts for feeding to obtain essential nutrients. Host feeding is the consumption of host fluids exuding from a wound, which is usually made by the female ovipositor (Jervis and Kidd, 1986). Host feeding is rare in pro-ovigenic parasitoids, where eggs are fully developed at the moment the female hatches (Jervis et al., 2001). For example, host feeding usually occurs in *En. formosa* (synovigenic; van Lenteren et al., 1987) but is rare in *A. fuscipennis* MacGown and Nebeker (Hym; Platygasteridae) (pro-ovigenic; de Vis et al., 2003).

As host feeding may result in killing of the hosts, a parasitoid female may select lower quality hosts for feeding and higher quality hosts for egg laying. Consequently, the female must make a decision whether to use a host for egg laying or for host feeding (Godfray, 1994). Host feeding is often more time consuming than egg laying (Heimple and Collier, 1996), and due to the difficulty of puncturing old nymphal instars, host feeding may occur more frequently on younger nymphs than on older ones (Kidd and Jervis, 1991).

The time budgets spent on foraging, and the kind of host-selection and feeding behavior should be considered to determine parasitoid effectiveness and to select the best species for biological control (e.g., Drost et al., 2000; Hudak et al., 2003). So far, some aspects of host-searching and host-handling of *E. eremicus* and/or *E. mundus* have been studied (e.g., Foltyn and Gerling, 1985; Headrick et al., 1996; Drost et al., 2000; Hudák et al., 2003; Qiu et al., 2004). However, much information about these behaviors is still incomplete. Therefore, we embarked upon a study of *Eretmocerus* to compare host-handling behavior between two arrhenotokous species (Spanish *E. mundus* and North American *E. eremicus*) and between an arrhenotokous (Spanish *E. mundus*) and a thelytokous population (Australian *E. mundus*). The results are discussed within the framework of biological control of whitefly.

Material and methods

Maintenance of insects

A culture of *B. tabaci* was maintained on poinsettia plants (*Euphorbia pulcherrima* Willd. ex Klotzsch, Euphorbiaceae) in a greenhouse (25 °C, 75% RH, and 16L/8D light). Poinsettia plants were daily infested with 20–30 whiteflies and put in a cage. Whitefly infested plants were transferred to another cage after two days while the whiteflies were removed. Leaves of these plants were checked after 10–12 days and leaves with the right whitefly stages were removed and used in experiments.

Three populations of *Eretmocerus* were used: (1) an arrhenotokous population of *E. eremicus* (origin North America), (2) an arrhenotokous population of *E. mundus* (origin Spain) that are both commercially available (product name ErCal[®], Koppert Biological Systems, The Netherlands), and (3) a thelytokous population of *E. mundus* (origin Australia), which is a non-commercial laboratory population (de Barro et al., 2000). A culture of each parasitoid population was maintained on *B. tabaci* and poinsettia plants in a climate room at 25 ± 1 °C, 45 ± 5% HR, and a 16L/8D photo period.

All experiments were done in a climate room at 25 ± 1 °C, 45 ± 5% HR.

Host-handling behavior

Infested leaf parts (4 cm × 5 cm) with a mixture of different *B. tabaci* nymphal instars (N1, N2, and N3) were offered to the parasitoids. A preliminary experiment had shown that *Eretmocerus* did not accept N4 for oviposition, so N4 nymphs were not offered in the current experiments (Ardeh, unpublished results). Each leaf part was put in a Petri dish (11 cm Ø) on a moist piece of cotton wool to prevent desiccation.

Parasitoid pupae were collected and put separately in a glass vial until they had emerged. Females were always used on the first day of emergence. To obtain mated females of arrhenotokous populations, males and females were released on an uninfested leaf part before the experiment until mating had taken place. Next, either a mated arrhenotokous or an asexual thelytokous female was released on an infested leaf part, and their foraging behaviors were recorded using a stereo microscope and The Observer Program 4.0[®] (Noldus, Information Technology) for a period of maximum 1 h or until the female left the leaf part. The following behavioral elements were recorded (Figure 1):

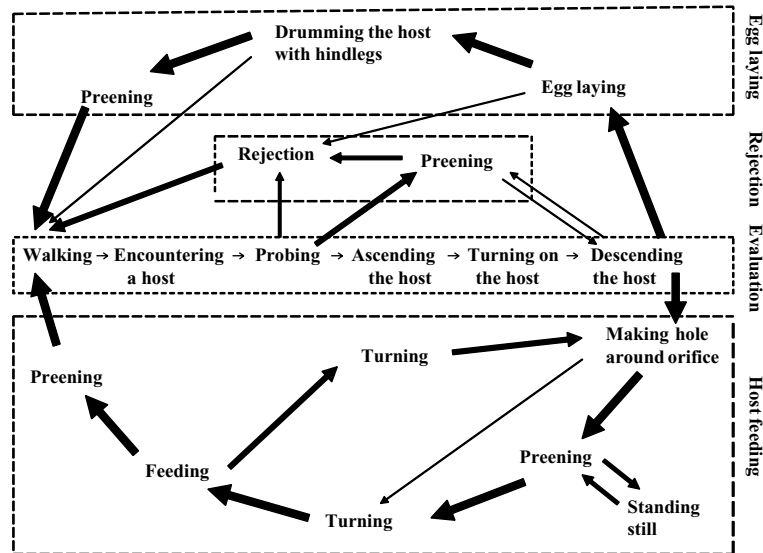


Figure 1. Generalization of the sequence of three basic behaviors (evaluation, egg laying, rejection and host feeding) of *E. mundus* (arrhenotokous and thelytokous) and *E. eremicus* (arrhenotokous) after encountering *B. tabaci* nymphs. The thickness of the arrows reflects the general frequency of transitions between the behaviors.

walking, standing still, preening (parasitoid cleans her body), encountering (the first contact with the host by the antennae of the parasitoid), probing (parasitoid drums the host with the antennae), ascending (parasitoid climbs on the host), descending and laying egg (moves down from the host and inserts the ovipositor under the host), and feeding of host or honeydew. Each experiment consisted of enough replications to include at least 20 ovipositions under each nymphal instar of *Bemisia* with *E. mundus* by each of the three parasitoid populations.

Data analysis

The data were analyzed with a general linear model (GLM procedure in SAS).

Results

Female behavior on the leaf parts (standing still, walking, preening or feeding on honey) showed substantial variation in frequency and duration (Figure 2). However, females always showed three basic

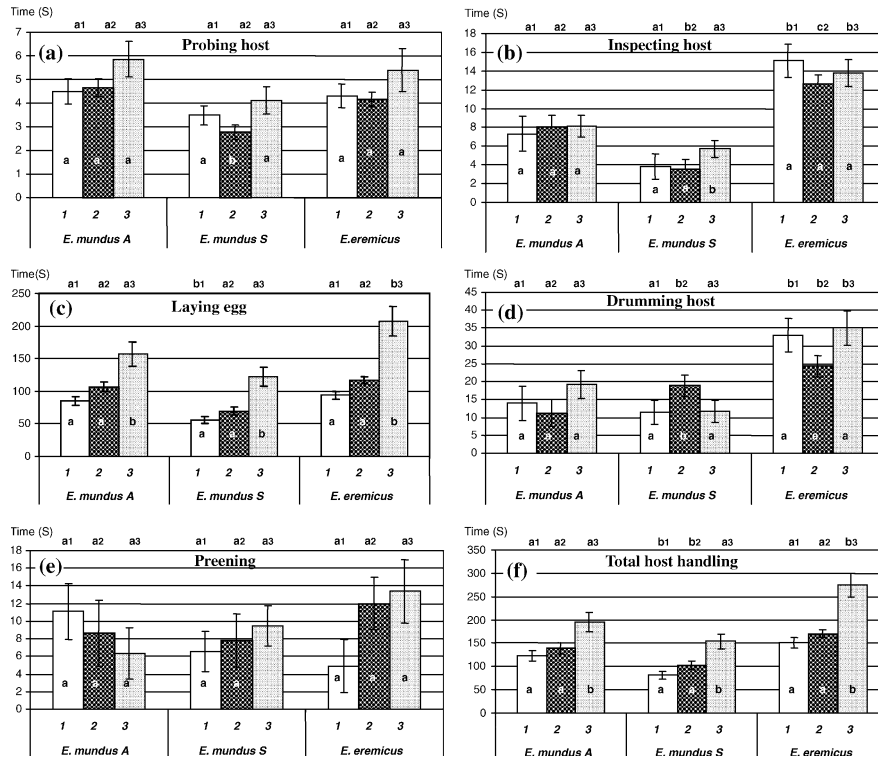


Figure 2. Mean duration (\pm S.E.) of different behaviors of *E. mundus* and *E. eremicus* females after encountering different stages of *Bemisia* nymphs (N1, N2, and N3, indicated by 1–3, respectively, on horizontal axis). Statistical comparisons were made of means between populations/species for each nymphal instar separately (significant differences are indicated by different letters above the bars), and between nymphal instars for each species/population separately (significant differences are indicated by different letters in the bars). A = Australia and S = Spain.

sequences of behaviors upon encountering a host: egg laying, host feeding, and host rejection (Figure 1).

Acceptance of hosts for egg laying

Females of all populations showed the same sequence of behaviors to select a host for egg laying

1. Probing the host with the antennae.
2. Ascending the host and inspecting its periphery with antennae.
3. Descending, inserting the ovipositor under the host, and laying an egg.

4. Withdrawing the ovipositor and drumming the dorsal part of the host with the hind legs.
5. Preening (antennae and fore legs) and walking away.

No correlations were found between durations of corresponding phases of host-handling behavior across parasitoid populations/species or host nymphal instars (all tests gave insignificant Pearson Correlation Coefficients, data not shown).

The probing phase had the shortest duration compared with other host-handling behaviors, and lasted on average about 4 s. (Figure 2a). There were no significant differences in the duration of this behavior either between different parasitoid populations/species or between different host nymphal instars, except for the second nymphal instar in *E. mundus* where the duration of probing was significantly shorter.

During the second host-handling phase, the parasitoids climb on the host and turn on it while drumming. The females presumably then probed for a proper place to lay an egg under the host. As soon as they found such a place they descended from the host. The duration of this probing phase was on average between 2 and 15 s. (Figure 2b), and was not significantly different among different host nymphal instars (except for N3 in *E. mundus* from Spain where it was longer). However, it was significantly longer in *E. eremicus* than in the two *E. mundus* populations (Table 1).

The third phase during which oviposition takes place, had the longest duration of all host-handling behaviors (on average between 50 and 220 s.; Figure 2c) and was significantly longer on third nymphal instars than on younger ones (Table 1). The duration of oviposition was in most cases not significantly different between parasitoid populations/species, except for oviposition under the 3rd NS (nymphal stage) by *E. eremicus* (longest) and under 1st NS by Spanish *E. mundus* (shortest).

During the fourth phase, and immediately after having laid an egg, parasitoids started drumming the host with the hind legs and this phase lasted between 10 and 35 s. (Figure 2d). Duration of this phase was significantly longer in *E. eremicus* than in both *E. mundus* populations (Table 1).

In the last phase of host handling, females preened the antennae and the head during an average of 5–14 s. (Figure 2e) and then walked away from the host. For this phase, no significant differences in handling times were found (Table 1).

The total host-handling time for laying an egg lasts between 80 and 275 s., and variation is largely explained by that of the time needed for oviposition (Figure 2f).

Table 1. Duration of different phases of host-handling behavior among populations of *Eretmocerus* and three nymphal instars (N1, N2, N3) of *Bemisia*

	Differences among different nymphal instars						Differences among different species					
	<i>E. mundus</i> A		<i>E. mundus</i> S		<i>E. eremicus</i>		Egg laying N1		Egg laying N2		Egg laying N3	
	F _(60;2)	Pr > F	F _(102;2)	Pr > F	F _(74;2)	Pr > F	F _(77;2)	Pr > F	F _(92;2)	Pr > F	F _(62;2)	Pr > F
Enc	1.59	0.21	2.32	0.10	1.72	0.19	1.48	0.23	8.80	0.00	1.91	0.16
Turn	0.13	0.88	3.98	0.02	0.99	0.38	12.56	0.00	21.35	0.00	11.46	0.00
Egg	9.95	0.00	16.98	0.00	18.64	0.00	12.67	0.00	17.83	0.00	4.87	0.01
Drum	0.36	0.26	8.39	0.00	1.27	0.29	7.53	0.00	3.89	0.02	8.31	0.00
Preen	0.51	0.60	0.82	0.44	1.00	0.37	1.08	0.34	0.55	0.58	1.15	0.32
TH	7.24	0.00	17.48	0.00	10.03	0.00	14.13	0.00	14.04	0.00	8.47	0.00

The bold numbers indicate significant differences. Enc = encounter, Turn = turn on host by female parasitoid, Egg = egg laying, Drum = drumming the host with the hind legs, Preen = preening the antennae, TH = total duration of host handling for egg laying, A = Australian and S = Spanish.

Acceptance of hosts for feeding

Females showed the same probing and ascending behavior for host feeding as for egg laying, but instead of laying an egg, they tried to make a wound with their ovipositor in the orifice region of the *Bemisia* nymphs. Females normally tried two, three or even four times to make a wound, and each time they showed the following sequence of behaviors: preening, turning, probing the wound, and then either feeding from host or turn again for a new attempt to make a wound. Females of the *Eretmocerus* populations/species accepted the three youngest nymphal stages for host feeding. During feeding females fed on the haemolymph of the host, which eventually resulted in killing the host. In both *E. mundus* strains, the frequencies of attempts to make a wound were lower and the total duration of making a wound was shorter in nymphal instars 1 and 2 than in nymphal instar 3 (Figure 3a). For *E. eremicus* there was no difference in number of attempts to make a wound and host-feeding duration (Figure 3a). The duration of host feeding tended to increase with host stage and was shorter for *E. mundus* populations than for *E. eremicus* (Figure 3b). However, due to the infrequent occurrence of host feeding, the number of observations was too low to allow meaningful statistical analysis of its duration.

Rejection of hosts

Most rejections took place at the end of each observation, and *E. eremicus* rejected more hosts in the course of time than *E. mundus* populations (Figure 4). Females did not show any bias among encountered host stages and rejections occurred for all different nymphal instars. When a female did not accept a host, it rejected it either at

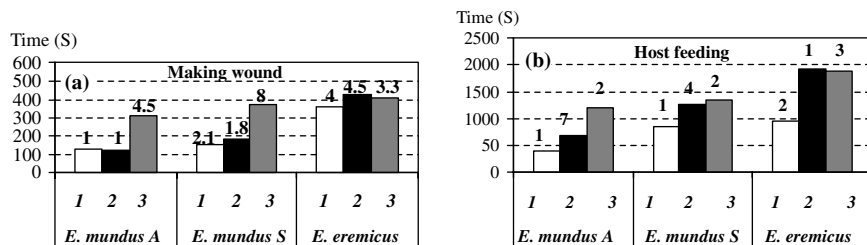


Figure 3. Duration of making a wound and host feeding in *E. mundus* and *E. eremicus* on different nymphal instars of *B. tabaci* (N1, N2, and N3, indicated by 1–3 respectively, on horizontal axis). A = Australia and S = Spain.

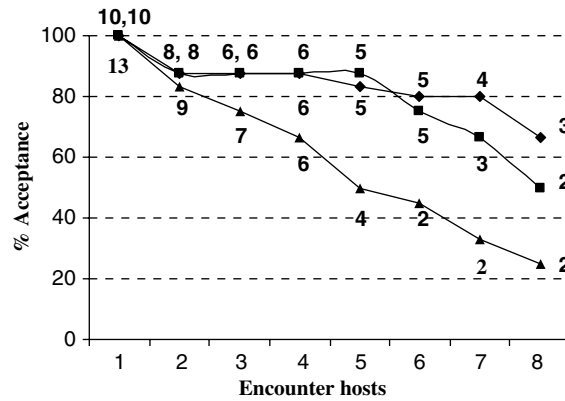


Figure 4. Mean percentage acceptance of hosts (*B. tabaci* nymphs) during foraging by *E. mundus* (two strains) and *E. eremicus*. The number of females still foraging is given above each data point; *E. mundus* Spain (= ◆), *E. mundus* Australia (= ■), *E. eremicus* (= ▲).

first touch with the antennae or after drumming the nymph with the antennae, a behavioral component which lasted from less than 1–2 s.

Discussion

Parasitoids of many species show typical host-handling behavior that can be described by particular phases and sequences (Vinson, 1998). Earlier, *Eretmocerus* host-handling behavior has been divided in three phases (Foltyn and Gerling, 1985; Headrick et al. 1996). Based on our new observations we propose to divide this behavior into five phases: (1) probing the host with the antennae, (2) ascending and turning on the host, (3) descending, inserting the ovipositor and egg laying, (4) drumming the host with the hind legs, and (5) preening antennae and fore legs.

Actual oviposition (phase 3) had the longest duration amongst host-handling behaviors. The duration was significantly longer in third instar nymphs than in younger ones, which might be due to the difficulty of inserting the ovipositor under the host. Foltyn and Gerling (1985) stated that females put their wings in a vertical position when they lay an egg. However, we could record this behavior only a few times. Our interpretation is that in these cases the females use more force to insert the ovipositor under the host.

After oviposition, many species of parasitoids mark the parasitized host to avoid parasitizing it again (van Lenteren, 1981; Godfray, 1994;

Vinson, 1998; Nufio and Papaj, 2001). *Eretmocerus* females started drumming the host with the hind legs after oviposition, and with this drumming we suppose that they apply a chemical mark.

Foltyn and Gerling (1988) reported that *E. mundus* prefers third instar nymphs for oviposition. In contrast, Headrick et al. (1996) found that *E. eremicus* did not show a particular preference for any nymphal instar. We found that all three nymphal instars were accepted for egg laying in the sequence as encountered, and a preference for certain host nymphal instars was found neither for *E. mundus* populations, nor for *E. eremicus*.

The three youngest nymphal instars were also accepted for host feeding by *Eretmocerus* females after making a wound in the orifice region of the host. Some authors consider surface feeding on hosts as host feeding (Headrick et al., 1996). However, in this study we only recorded host feeding sensu stricto, which only took place after making a wound. Jervis and Kidd (1986) distinguished four different types of host feeding: (1) concurrent feeding, where parasitoids use the same host for feeding and oviposition; (2) non-concurrent feeding, where different hosts are used either for egg laying or host feeding; (3) destructive host feeding, where hosts die because of feeding; (4) non-destructive host feeding, where hosts survive after feeding. As feeding by *E. mundus* and *E. eremicus* in our tests always resulted in killing of the hosts, host feeding in *Eretmocerus* can be described as non-concurrent and destructive. The finding that *Eretmocerus* females use a host either for oviposition or for feeding has been reported for other aphelinids as well (van Lenteren et al., 1980; Gerling, 1990; Headrick et al., 1996).

The *Eretmocerus* ovipositor is not as hard and sharp as that of *Encarsia*, which lays eggs inside the host (Gerling et al., 1998). Therefore, the *Eretmocerus* females select a soft part of the body in the orifice region to make a wound for host feeding. However, Jervis et al. (2001) stated, 'it needs to be established whether the females consume mainly the host's haemolymph or mainly the honeydew contained in the host's hind gut'. Our observations showed that *Eretmocerus* females spent a lot of time to make a wound in the host and consumed nearly all haemolymph of the host, resulting in an empty exoskeleton of the host. Thus, it is clear that *Eretmocerus* females feed on the haemolymph rather than on honeydew.

As *Eretmocerus* females did not show preference for one of the youngest three host instar stages and these three stages were rejected equally, it seems that rejection of a host is more influenced by internal parasitoid factors (e.g., egg load) rather than a specific host stage. Females rejected parasitized hosts after the first touch of the host with

their antennae. Therefore, we suppose that *Eretmocerus* uses chemical cues for recognition of parasitized hosts.

Selection of Eretmocerus species/populations for biological control

Some variation occurred in the duration of the different phases of host-handling behavior between populations/species of *Eretmocerus*, but the differences were small and often insignificant. Further, all females equally well accepted all nymphal instars either for egg laying or for host feeding. The different mode of reproduction (thelytoky or arrhenotoky) of the *E. mundus* populations did not influence the duration of host-handling behavior for oviposition and host feeding. Hence, the small differences in host-handling behavior are unlikely to affect the biological control efficiency of populations/species of *Eretmocerus*. The longer host-handling times and the higher host-rejection rate of *E. eremicus* (Figure 4) might make this species slightly less efficient. Taking all current data into consideration, the thelytokous population of *E. mundus* from Australia may be the best candidate for control of *Bemisia*, if the host-location capability and fecundity of the thelytokous population is similar to that of arrhenotokous populations. These characteristics form the topic of our next study.

Acknowledgements

We are grateful to Dr. P.J. de Barro (CSIRO Entomology, (CSIRO Entomology, 120 Meiers Road, Indooroopilly, Qld 4068, Australia) for providing an Australian population of *Eretmocerus mundus*, and to Koppert Biological Systems and Biobest Biological Systems for providing the other *Eretmocerus* populations. M.J. Ardeh received financial support of the Agricultural Ministry of Iran.

References

- Casas, J., R.M. Nisbet, S. Swarbrick and W.W. Murdoch, 2000. Eggload dynamics and oviposition rate in a wild population of a parasitic wasp. *J. Anim. Ecol.* 69: 185–193.
- de Barro, P.J., P.J. Hart and R. Morton, 2000. The biology of two *Eretmocerus* spp. (Haldeman) and three *Encarsia* spp. (Hymenoptera: Aphelinidae) Forster and their potential as biological control agents of *Bemisia tabaci* biotype B (Homoptera: Aleyrodidae) in Australia. *Entomol. Exp. Appl.* 94: 93–102.
- de Vis, R.M.J., H. Mendez and J.C. van Lenteren, 2003. Comparison of foraging behavior, interspecific host discrimination, and competition of *Encarsia formosa* and *Amitus fuscipennis*. *J. Insect Behav.* 16: 117–152.

- Drost, Y.C., J.C. van Lenteren and H.J.W. van Roermund, 1998. Life history parameters of different biotypes of *Bemisia tabaci* (Hemiptera: Aleyrodidae) in relation to temperature and host plant: a selective review. *Bull. Entomol. Res.* 88: 219–229.
- Drost, Y.C., Y.T. Qiu, C.J.A.M. Posthuma Doodeman and J.C. van Lenteren, 1999. Life history and oviposition behavior of *Amitus bennetti* a parasitoid of *Bemisia argentifolii*. *Entomol. Exp. Appl.* 90: 183–180.
- Drost, Y.C., Y.T. Qiu, C.J.A.M. Posthuma Doodeman and J.C. van Lenteren, 2000. Comparison of searching strategies of five parasitoid species of *Bemisia argentifolii* Bellows & Perring (Homoptera: Aleyrodidae). *J. Appl. Entomol.* 124: 105–112.
- Foltyn, S. and D. Gerling, 1985. The parasitoids of the aleyrodid *Bemisia tabaci* in Israel: development, host preference and discrimination of the Aphelinid wasp *Eretmocerus mundus*. *Entomol. Exp. Appl.* 38: 255–260.
- Gerling, D., 1990. Natural enemies of whiteflies: predators and parasitoids. In: D. Gerling, (ed), *Whiteflies, their bionomics, pest status and management*, Intercept, Andover UK, pp.147–186.
- Gerling, D. and R.T. Mayer, 1995. *Bemisia: Taxonomy, Biology, Damage, Control and Management*. Intercept Andover UK.
- Gerling, D., O. Alomar and J. Arno, 2001. Biological control of *Bemisia* using predators and parasitoids. *Crop. Prot.* 20: 779–799.
- Gerling, D., D.L.J. Quicke and T. Orion, 1998. Oviposition mechanisms in the whitefly parasitoids *Encarsia transvena* and *Eretmocerus mundus*. *BioControl* 43: 289–297.
- Godfray, H.C.J., 1994. *Parasitoids*. Princeton University Press, Chichester, West Sussex,
- Headrick, D.H., T.S. Jr. Bellows and T.M. Perring, 1996. Behaviors of female *Eretmocerus* sp. nr. *californicus* (Hym.Aphelinidae) attacking *Bemisia argentifolii* (Homoptera: Aleyrodidae) on cotton, *Gossypium hirsutum*, (Malvaceae) and melon, *Cucumis melo* (Cucurbitaceae). *Biol. Control.* 6: 64–75.
- Heimpel, G.E. and T.R. Collier, 1996. The evolution of host feeding behavior in insect parasitoids. *Biological Reviews.* 71: 373–400.
- Higuchi, H. and Y. Suzuki, 1996. Host handling behavior of the egg parasitoid *Teleonomus triptus* to the egg mass of the stink bug *Piezodorus hybneri*. *Entomol. Exp. Appl.* 80: 475–479.
- Hodde, M.S. and R. van Driesche, 1999. Evaluation of *Eretmocerus eremicus* and *Encarsia formosa* (Hymenoptera: Aphelinidae) Beltsville strain in commercial greenhouses for biological control of *Bemisia argentifolii* (Homoptera: Aleyrodidae) on colored poinsettia plants. *Florida Ent.* 82: 556–569.
- Hudak, K., J.C. van Lenteren, Y.T. Qiu, and B. Penzes, 2003. Foraging behavior of parasitoids of *Bemisia argentifolii* on poinsettia. *Bull. Insectology* 56: 259–267.
- Jervis, M.A. and N.A.C. Kidd, 1986. Host feeding strategies in hymenopteran parasitoids. *Biological Reviews* 61: 395–434.
- Jervis, M.A., G.E. Heimpel, P.N. Ferns, J.A. Harvey and N.A.C. Kidd, 2001. Life history strategies in parasitoid wasps: a comparative analysis of 'ovigeny'. *J. Anim. Ecol.* 70: 442–458.
- Kidd, N.A.C. and M.A. Jervis, 1991. Host feeding and oviposition by parasitoids in relation to host stage. *Res. Popul. Ecol.* 33: 13–28.
- Lewis, W.J., L.E.M. Vet, J.H. Tumlinson, J.C. van Lenteren and D.R. Papaj, 1990. Variations in parasitoid foraging behavior: essential element of a sound biological control theory. *Environ. Entomol.* 19: 1183–93.

- Manzano, M.R., J.C. van Lenteren, C. Cardona and Y.C. Drost, 2000. Developmental time, sex ratio and longevity of *Amitus fuscipennis* MacGown and Nebeker (Hymenoptera: Platygasteridae) on the greenhouse whitefly. *Biol. Control*. 18: 94–100.
- Manzano, M.R., J.C. van Lenteren and C. Cardona, 2002. Searching and oviposition behavior of *Amitus fuscipennis*, a parasitoid of the greenhouse whitefly. *J. Appl. Entomol.* 126: 528–533.
- Mound, L.A. and S.H. Halsey, 1978. *Whitefly of the World*. Wiley, New York.
- Nuño, C.R. and D.R. Papaj, 2001. Host marking behavior in phytophagous insects and parasitoids. *Entomol. Exp. Appl.* 99: 273–293.
- Palumbo, J.C., A.R. Horowitz and N. Prabhakar, 2001. Insecticidal control and resistance management for *Bemisia tabaci*. *Crop Prot.* 20: 739–765.
- Qiu, Y.T., J.C. van Lenteren, Y.C. Drost and C.J.A.M. Posthuma Doodeman, 2004. Life history parameters of *Encarsia formosa*, *Eretmocerus eremicus* and *E. mundus*, aphelinid parasitoids of *Bemisia argentifolii* (Homoptera: Aleyrodidae). *Euro. J. Entomol.* 101: 83–94.
- Rodriguez, M.D., R. Moreno, M.M. Tellez, M.P. Rodry guez and R. Fernandez, 1994. *Eretmocerus mundus* (Mercet), *Encarsia lutea* (Masi) y *Encarsia transvena* (Timberlake) (Hym., Aphelinidae) parasitoides de *Bemisia tabaci* (Hom., Aleyrodidae) en los cultivos hortícolas protegidos almerienses. *Boletín Sanidad Vegetal Plagas*. 20: 695–702.
- Rose, M. and G. Zolnerowich, 1997. *Eretmocerus* Haldeman (Hymenoptera: Aphelinidae) in the United States with descriptions of new species attacking *Bemisia (tabaci complex)* (Homoptera: Aleyrodidae). *Proc. Entomol. Soc. Wash.* 99: 1–27.
- Stouthamer, R., 1993. The use of sexual versus asexual wasps in biological control. *Entomophaga*. 38: 3–6.
- van Driesche, R.G. and T.S. Jr. Bellows, 1996. *Biological Control*. Chapman and Hall, New York.
- van Lenteren, J.C., 1981. Host discrimination by parasitoids. In: D.A. Nordlund, R.L. Jones, W.J. Lewis (eds) *Semiochemicals: Their Role in Pest Control*, Wiley and Sons, New York. pp. 153–179.
- van Lenteren, J.C., 2000. A greenhouse without pesticides: fact of fantasy? *Crop Protection*. 19: 375–384.
- van Lenteren, J.C., H.W. Nell, L.A. Sevenster Vander Lelie and J. Woets, 1976. The parasite host relationship between *Encarsia formosa* (Hymenoptera: Aphelinidae) and *Trialeurodes vaporariorum* (Homoptera: Aleyrodidae). I. Host finding by the parasite. *Entomol. Exp. Appl.* 20: 123–130.
- van Lenteren, J.C., H.W. Nell and L.A. Sevenster Vander Lelie, 1980. The parasite host relationship between *Encarsia formosa* (Hymenoptera: Aphelinidae) and *Trialeurodes vaporariorum* (Homoptera: Aleyrodidae). IV. oviposition behavior of the parasite, with aspects of host selection, host discrimination and host feeding. *J. Appl. Entomol.* 89: 442–454.
- van Lenteren, J.C., A. van Vianen, H.F. Gast and A. Kortenhoff, 1987. The parasite host relationship between *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) and *Trialeurodes vaporariorum* (Westwood) (Homoptera: Aleyrodidae) XVI. food effects on oogenesis, oviposition, life span and fecundity of *Encarsia formosa* and other hymenopterous parasites. *J. Appl. Entomol.* 103: 69–84.
- van Lenteren, J.C. and L.P.J.J. Noldus, 1990. Behavioural and ecological aspects of whitefly- plant relationships. In: D. Gerling (ed) *Whiteflies: Their Bionomics, Pest Status and Management*. Intercept, Andover. pp. 47–89.

- van Lenteren, J.C., Y.C. Drost, H.J.W. Roermund, C.J.A.M. Van and Postuma Doodeman, 1997. Aphelinid parasitoids as sustainable biological control agents in greenhouses. *J. Appl. Entomol.* 121: 473–458.
- Vinson, S.B., 1998. The general host selection behavior of parasitoid hymenoptera and a comparison of initial strategies utilized by larvaphagous and oophagous species. *Biol. Control.* 11: 79–96.