



Bionomics of *Encarsia scapeata* Rivnay (Hymenoptera: Aphelinidae), tritrophic relationships and host-induced diapause

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ABSTRACT

During a survey of whitefly parasitoids in the Israeli Mediterranean forest, we found *Encarsia scapeata* Rivnay to be the only parasitoid of *Trialeurodes lauri* Signoret, growing on *Arbutus andrachne* L. trees. Overall parasitism levels averaged about 10% during the two-year study and correlated inversely with whitefly abundance. Following bud burst, the univoltine whiteflies oviposit on the young leaves (April–May), develop to the early 4th instar and then diapause from May–June to next spring, when their development to mature adults continues. Following a diapause that had apparently been induced by the whitefly host, most adult parasitoids emerged during April, intimately synchronized with their whitefly host. Natural diapause of the whiteflies and the wasps could be experimentally broken by cutting infested branches and keeping them under room conditions. Analyses of slide-mounted material revealed that parasitoid development usually occurred following initiation of post-diapause development in the unparasitized whiteflies of the same age, but occasionally preceded it. This host-dependent phenological plasticity of *E. scapeata* ensures synchronization with its hosts in the heterogeneous forest environment. In a lab set-up, *E. scapeata* readily parasitized the non-diapausing whitefly *Bemisia tabaci* (Gennadius), in which it too did not diapause. Thus, the diapause of *E. scapeata* is apparently induced by the diapause of its whitefly host. Since it can successfully develop on *B. tabaci*, *E. scapeata*, with its flexible developmental strategy, could serve as an addition to the pool of *Encarsia* species useful for *B. tabaci* control.

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1. Introduction

Synchronization between resource availability and developmental phases across all three trophic levels is crucial for continuous development and stability. In herbivores and in their natural enemies that are linked to the phenology and availability of their host plants, synchronization might include adaptations of the exploiting, higher trophic level, organism to the physiological and phenological cycles of the exploited host, such as plant dormancy or prey and host diapause (Crawley, 1992; Godfray, 1994; Jervis and Kidd, 1986; Schoonhoven et al., 1998). Such adaptations are necessary both under naturally occurring tritrophic interactions and in biological control projects that follow man's intervention, if they are to be stable and bring about successful control. During the present study, following a survey of parasitoids attacking whiteflies on natural vegetation, we studied the synchronization in such a tritrophic system that comprises the tree *Arbutus andrachne*, the herbivorous whitefly *Trialeurodes lauri* Signoret and its parasitoid *Encarsia scapeata* Rivnay in Israel (Erel, 2004; Gelman et al., 2005).

Whitefly parasitoids of the genus *Encarsia* oviposit within the host, usually in nymphal instars 2–4 and, following 3 molts, they pupate within the empty host skin. Life cycles typically last about 15–30 days, depending upon the species and temperature. Most species have divergent ontogenies of the sexes with many being autoparasitic, i.e., males develop at the expense of other whitefly-parasitizing immatures (Hunter and Woolley, 2001).

The evergreen tree *A. andrachne* is well adapted to the hot, dry summers and cold, rainy winters of the Mediterranean climate. It foliates in the spring (mostly March–May) and then (May–June) sheds the leaves of the previous year, keeping the recently formed foliage until next year. The univoltine, oligophagous whitefly *T. lauri* emerge, land *en masse* and settle during April and May on the young foliage (Erel, 2004; Gelman et al., 2005), where they oviposit. They develop rapidly to the early 4th instar nymphs at which stage they diapause until early the next spring, when they develop to adulthood.

Many species of whiteflies have been successfully controlled through biological control efforts, most of which involve the use of parasitoids (Gerling, 1990; Gerling et al., 2004; Onillon, 1990). Other species, including the tobacco or sweet potato whitefly *Bemisia tabaci* (Gennadius), are still the subject of search for better controlling agents. The list of parasitoid species that attack other

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whitefly species, but might be candidates for *B. tabaci* control, continues to increase (Gerling et al., 2001). A better understanding of the bionomics of such species, in particular if they have been proven to develop also on *B. tabaci*, might serve in the search for potential biological control agents. Here we report the result of our studies of *E. scapeata* bionomics, in particular the apparent influence of tree dormancy on the tritrophic relationships. We also examine the capacity of this, host specific parasitoid, to adapt to the non-diapausing whitefly pest, *B. tabaci*.

2. Materials and methods

2.1. Parasitoid populations in the field

Monthly field observations and collection of whiteflies and parasitoids were carried out on 22 marked *A. andrachne* trees in the Nahal Ktalav nature park (ca. 25 km south-west of Jerusalem, with temperature in winter ranging ~2–22 °C and in summer ~15–30 °C) from March 2002 till January 2004. Visit frequency increased to ca. once every 10 days during the emergence and oviposition period (March–June). In addition, the density of the adult whiteflies and parasitoids was monitored by counting the catches on nine yellow sticky traps (16 × 20 cm) suspended from the tree canopy (ca. 1 m above ground) and replaced during each visit. Significance of the correlations between whitefly numbers and parasitoids on the leaf and on sticky traps was examined using Spearman Rank Correlation tests (Sokal and Rohlf, 1981).

Parasitism levels per leaf were evaluated from 319 leaves (145/174 for 2002 and 2003, respectively) collected during April and May, when parasitism could easily be observed through the transparent whitefly skin, eliminating the need for dissections. Likewise, the relationship between parasitoid and host density was examined by sampling 615 whitefly-infested leaves collected from all 22 trees during April and May. The development of the whiteflies and parasitoids kept in the sleeve cages served for following their dynamics and their dependence upon the host tree throughout the season (see below).

2.2. Development of *E. scapeata*

Determinations of *E. scapeata* parasitism rates and developmental stages were made through observations of the whiteflies on the leaf, dissections and examination of slide-mounted preparations. Observations on the leaf were only useful during March to May, when development could easily be observed through the light-colored, transparent whitefly nymphs or from the presence of emergence holes. In order to determine parasitoid stages before March, when they are not easily seen with a dissecting microscope, dissections and whole mounts were performed. Two hundred whitefly nymphs/collection were dissected each month in a drop of water and examined for parasitoid immatures. The whole-mount microscope slides were prepared from all the whiteflies present on three–five infested leaves. For this purpose, the leaves were removed weekly from the day of collection on, from the monthly collected branches (see above). All whitefly nymphs were dislodged by dipping the leaves in Carnoy's fixative (Ref. Anonymous: [http](http://)). Slides were made, both as whole-mounts of the whiteflies and as sectioned material. The fixative was exchanged with absolute ethanol for about 2 h. The whiteflies were then run through two changes of Xylene (about 2 h) and, for whole mounts, were placed on a microscope slide in a drop of Permount®. For histological observations, the material was prepared, sectioned, mounted, deparaffinized and stained (see Blackburn et al., 2002). Whole mounts and sections were examined under a Wild M40 or a Nikon Eclipse 600 compound microscope. The latter was

equipped with Differential Interference Contrast optics and photomicrographs were taken using a Nikon DMX 1200 CCD camera. These served us to compare the developmental stages of the parasitoids within their hosts.

Whiteflies in the whole-mount slides were sorted according to their developmental stages: 1. flat nymphs with undeveloped compound eyes [corresponding to stage 4.1 of *T. vaporariorum* (Gelman et al., 2002)]; 2. initial, developed wing buds; 3. folded wing buds; 4. initial or complete eye development. We also determined the duration from collection to parasitoid emergence and parasitism rates (the latter in 2003 only).

Since most known species of *Encarsia* are autoparasitoids (Hunter and Woolley, 2001), we experimentally exposed both parasitized and unparasitized whitefly hosts to virgin and to mated parasitoid females and recorded the outcomes.

2.3. Plant dormancy and *E. scapeata* diapause

Following preliminary data analysis we decided to complement the data by collecting whole branches (ca. 70 cm long) once a month from November 2004 to December 2005; these were held in water within sleeve cages. From each branch collection, one cage was held in an incubator (27 °C, 14 h light) and another in the laboratory room (15–25 °C and normal outside light with day length fluctuating between 10/14 and 14/10 day/night regime). They were kept till the leaves had either dried up or all whitefly and parasitoids had emerged (ca. 1 month).

2.4. Development of *E. scapeata* on *B. tabaci*, a non-diapausing whitefly

The stage and species of hosts acceptable for parasitization were examined by placing parasitoid females on lab-grown or field-collected whitefly nymphs at different instars. This was done both with the natural host *T. lauri* and a factitious host, *B. tabaci*. Preliminary observations indicated that *E. scapeata* readily oviposited in the non-diapausing *B. tabaci*. Consequently, a culture was set up using the emerging material.

3. Results

3.1. Parasitoid populations in the field

The 319 examined leaves contained 85,137 nymphs, out of which 11.2% were dead and 10.16% were parasitized. Most of the leaves supported 1–20% parasitism (Fig. 1), with five leaves bearing 1–44 whiteflies and showing 100% parasitism, and 44 leaves with

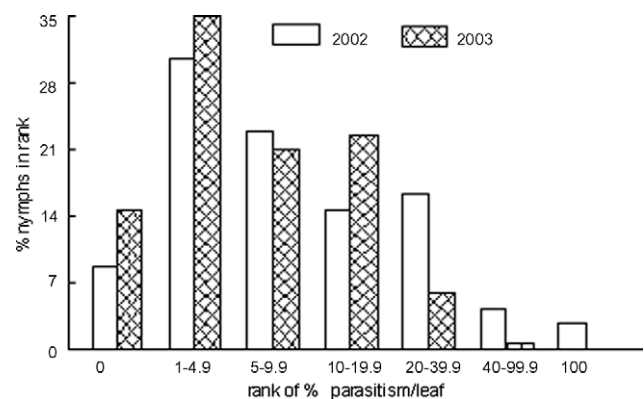


Fig. 1. Frequency distribution of field parasitoid emergence rates of *T. lauri* by *E. scapeata* in 2002 and 2003 ($N = 319$), ranked by density groups per leaf.

7–457 whiteflies not parasitized at all. All mature wasps emerged within 3 months (March–May) with monthly emergence rates ranging between 6.48% and 15.23% (Fig. 2). Parasitism rates on the slide-mounted material were much lower: of 8266 counted whitefly nymphs, only 237 (2.9%) were found parasitized. Percentage parasitism declined significantly with the rise in nymph density per leaf (Fig. 3).

In lab observations, parasitoid females laid fertilized eggs in 2nd instar whitefly nymphs and rejected older ones. Between June and late December, only 1st instar parasitoid larvae were found in field collected material. The first 2nd instar larva was found on 27 December (five 1st instars and one 2nd instar) while in February both 2nd and 3rd instars were found in the dissections (Fig. 4) but only 2nd instars were seen in the slides (2 larvae in 107 hosts). During March, both dissections and mounts revealed 3rd instar larvae while dissections also exposed parasitoid prepupae (Fig. 4). Pupation and emergence of both sexes took place from March to May. Thus, the parasitoids both aestivate and hibernate as 1st instars, with the developmental cycle of the females lasting about 10–11 months in correspondence with the cycle of their whitefly hosts (Fig. 5).

3.2. Development of *E. scapeata*

The whole-mount slides of field-collected whiteflies and of those that had been incubated in the lab, showed parasitoid development from 1st to 2nd instar being usually concurrent with whitefly wing bud development. However, in some cases, the unparasitized whiteflies on the same leaf were all still in stage 4.1, when parasitoid stages up to the pupae were present (Table 1). Male development was at the expense of female immatures and occurred during the spring. The oviposition time of male-producing eggs has not been determined.

Exposure of virgin and mated females to parasitized and unparasitized hosts in the laboratory showed that male development is autoparasitic. Unfertilized females rejected unparasitized whitefly hosts while attempting to oviposit in parasitized ones in lab observations conducted in the spring. Moreover, when reared on *B. tabaci* males developed autoparasitically in the laboratory.

3.3. Plant dormancy and *E. scapeata* diapause

We found a significant positive correlation between numbers of adult whiteflies and parasitoids caught on the sticky traps (Fig. 6), both of which occurred mainly during April and May (Pearson

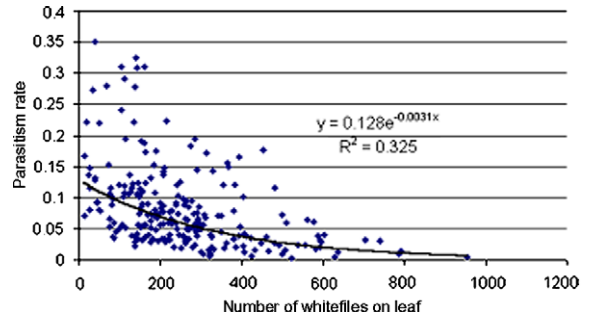


Fig. 3. A graph showing the negative correlation between parasitoid emergence rates and whitefly density on the leaves. Spearman Rank Order correlation; $r_s = -0.54$, $df = 238$, $p < 0.05$; $n = 239$ (Sokal and Rohlf, 1981).

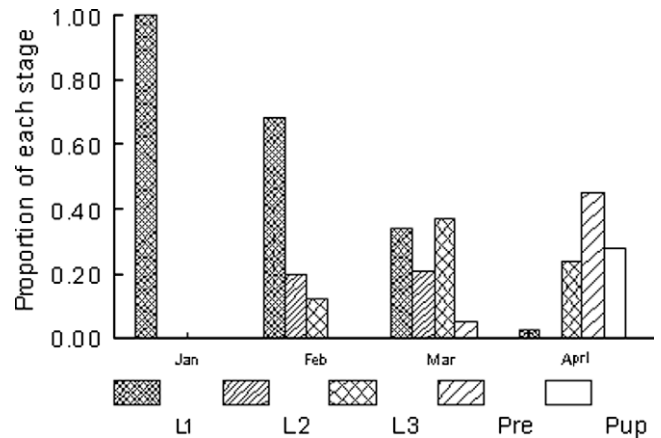


Fig. 4. Developmental stages of field collected *E. scapeata* dissected out of *T. lauri* January–May 2002–2003 ($N = 200$ hosts/month). L1–L3 designate larval stages, Pre = prepupae and Pup = pupa.

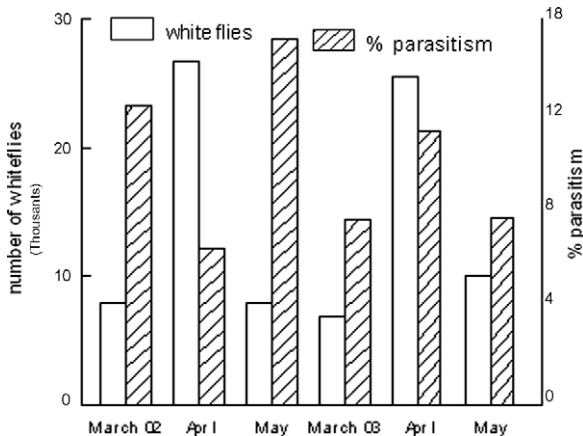


Fig. 2. Percentage parasitism and numbers of whiteflies emerging per month in the 319 examined leaves containing 85,137 nymphs examined during 2002–2003.

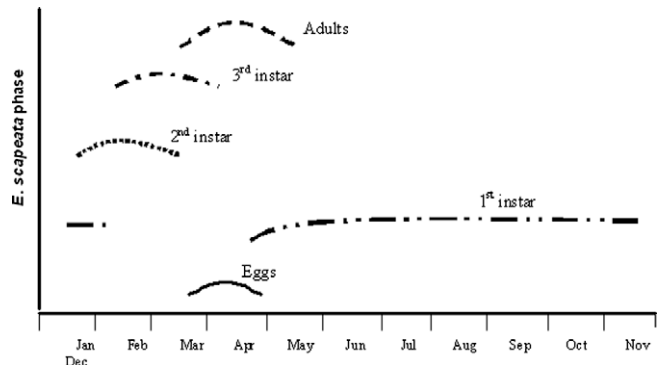


Fig. 5. A diagrammatic representation of the yearly cycle of *E. scapeata* developing on *T. lauri*.

$r = 0.865$; $df = 8$; $p < 0.01$). Examination of emergence holes on the leaves confirmed these findings.

Our qualitative sleeve-cage observations showed that, in contrast to the diapausing whiteflies and parasitoids in the field, individuals on the cut branches in both the room and incubator, continued developing to adulthood. Adult whitefly and parasitoid emergence was typically shorter by a few days in the incubator than that in the room. The time from branch cutting to emergence became shorter as the season progressed. In December, *E. scapeata* female emergence started 14 days after the branches were collected in the field, and in February and March time to emergence

Table 1
Parasitoid development in nymphs of *T. lauri* that have been collected on the 23rd of November 2002 and the 25th of January 2003 and were incubated in the lab. Data show different stages of *E. scapeata* development on different dates on which all unparasitized whiteflies were undeveloped (in stage 4.1).

Dates		Days kept in lab	Number ^a	Parasitoid stage (L = larval instar)			
Collected	Observed			L1	L2	L3	Pupa
23 Nov	23 Nov	0	285	0			
23 Nov	1 Dec	8	449	8	4		
23 Nov	7 Dec	14	83	2	3		
23 Nov	4 Jan	42	127	2	2	1	
25 Jan	25 Jan	0	195	5			
25 Jan	2 Feb	8	213		2	1	1

^aNumber of examined whitefly nymphs.

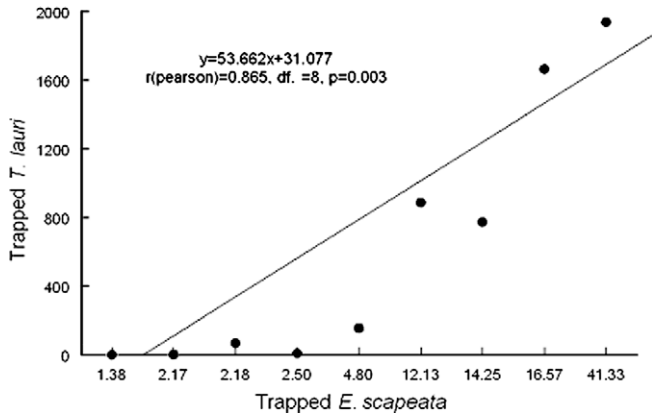


Fig. 6. Correlation between the adults of *T. lauri* and *E. scapeata* caught on sticky traps in three locations [Pearson Correlation $r = 0.865$; $df = 8$; $p < 0.01$].

was ca. 6 days. Material collected in late April and May produced parasitoids within one day. Males started to emerge about 10 days after first female emergence in the February collections and together with the females in the April–May collections.

3.4. Development of *E. scapeata* on a *B. tabaci*, a non-diapausing whitefly

Encarsia scapeata oviposited in nymphs of *B. tabaci*, producing viable progeny of females as primary parasitoids and of males as hyperparasitoids. These continued to reproduce on *B. tabaci* for several generations. Unlike the univoltine, year-long development on its natural host, the overall development on this non-diapausing factitious host lasted 21.6 ($n = 10$, range 19–25) days, showing no diapause.

4. Discussion

Encarsia scapeata was found to be the only parasitoid of *T. lauri* in Israel. Its life cycle is closely synchronized with that of its whitefly hosts and with the phenology of *A. andrachne* trees. Synchronization is achieved by diapausing for about 10 months within the 4th nymphal host stage (see also Erel, 2004; Gelman et al., 2005). The resulting univoltine life cycle is clearly phenotypic since continuous development occurred on the non-diapausing *B. tabaci*, a fact permitting us to add *E. scapeata* to the list of the latter's potential control agents.

4.1. Parasitoid–host relationships

4.1.1. Rates of parasitism

Parasitism rates as measured through counting emergence holes were only ca. 10% and those obtained through microscopic

host examination were lower still, reaching only ca. 3%. Since emergence holes are easily observed, whereas microscopic detection of the practically transparent 1st instar larvae is often difficult, we assume that the discrepancy between rates is due to errors in detection of parasitoid larvae in the slide-mounted material.

It is common to observe naturally occurring, undisturbed insect populations being controlled to some extent by their natural enemies, often by their parasitoids. In the case of *T. lauri* and *E. scapeata*, this does not seem to be the case. Despite appearance of the whiteflies by the hundreds/leaf, parasitism rates were low, and inversely density-dependent. Hence, *T. lauri* has been recorded as a pest in many regions of *A. andrachne* occurrence (Danzig, 1972).

4.1.2. Synchronization of life cycles

Diapause has been documented for numerous parasitoid species, including those of lepidopterous eggs and larvae (e.g., Boivin, 1994; Brown and Phillips, 1990; Milonas and Savopoulou-Soultani, 2000), psyllids (Mehrnejad and Copland, 2005), aphids (e.g., Polgár and Hardie, 2000), and beetles (Nechols et al., 1980). To our knowledge, the present findings are the only record of diapause occurrence in *Encarsia* species parasitizing whiteflies.

In nature, both whitefly and parasitoid development start about January. Severing the plant branches from the tree and placing them under laboratory conditions (with fluctuating temperature and a light regime identical to the field) or in an incubator (with constant temperature and illumination hours), seems to circumvent the developmental inhibition. These results (controlled for day-length and temperature) suggest that whitefly and parasitoid development are regulated by plant factors, which were truncated by our severing of the branches. It seems that in *E. scapeata* the importance of external factors (e.g., light and temperature), which have a direct effect on the tree and often control a parasitoid's entrance into and exit from diapause (e.g., Mehrnejad and Copland, 2005), might be overshadowed by the tree's dormancy cycle. Thus, although physical environmental conditions probably have a significant role in the entrance into and exit from diapause of the biological system with which we worked, the effect is probably induced in a bottom-up manner, with the tree's physiology overriding any additional environmental effect that might incur. Likewise, the consideration that the physiological condition of the parasitoid females prior to and at the time of oviposition influences the proportion of her progeny that enter diapause (Boivin, 1994; Milonas and Savopoulou-Soultani, 2000), is not relevant to our situation, with 100% of the *E. scapeata* parasitizing *T. lauri* going into diapause and 100% of those in *B. tabaci* avoiding it. Moreover, a study of the effect of the host instar on diapause initiation is precluded because only very young (2nd instar nymphs) of *T. lauri* are parasitized.

The physiological interactions that are associated with the synchronized diapause have not been studied. However, the development of the 2nd–3rd instars of the parasitoid in the developing 4th instar nymphs of the host is consistent with other *Encarsia* species

(Gelman et al., 2002). Our observations indicate that the responses of the *E. scapeata* females to changes in the host, leading to molting of the parasitoid larva from 1st to 2nd instar already in the early 4th whitefly instar differed from those found by Gelman et al. (2002) for *E. formosa*. Moreover, *E. scapeata* advanced, albeit only rarely, from its first (diapausing), to the 2nd and 3rd instars before the host showed wing-bud development. This indicated that the cues necessary to initiate the development of the 2nd and 3rd instars might differ in their nature or level from those acting in *E. formosa* (Gelman et al., 2002). Such cues might consist of novel chemical messengers perceived by the parasitoid, or of different sensitivities of the parasitoid to the chemicals, or to both.

Our results show the presence of a phenology-dependent association across the trophic levels: parasitoids, herbivores and plants, in nature. To ensure synchronization with its obligate whitefly host, *E. scapeata* have adopted a long, host-sensitive diapause. Thus, the wasps follow the univoltine life cycle of *T. lauri* as governed by the availability of suitable leaves produced by *A. drachne* trees once a year. The plasticity of the parasitoid's developmental cycle is demonstrated through the facultative nature of the parasitoid's diapause, which was skipped once a non-diapausing whitefly was used as a host.

4.2. Male production

Our results suggest that autoparasitic male production in the field could follow one of two paths (or both). First, since some parasitoid females develop faster than others (Table 1) and emerge already in March as virgins, they could parasitize developing parasitoid immatures in their 3rd instar or as still unsclerotized pupae, as shown by Gerling and Rejouan (2004) for *E. sophia*. The resulting males could potentially mate with the females emerging in late April and May. Alternatively, male-producing eggs might be laid already in the spring, in whiteflies that already contain female-producing eggs or young female larvae (Gerling and Rejouan, 2004).

The first scenario (males producing eggs are laid on female larvae and young pupae) conforms with the general pattern of autoparasitic development typical to most *Encarsia* species (Foltyn and Gering, 1987; Hunter and Kelly, 1998; Hunter and Woolley, 2001; Pedata and Hunter, 1996; Williams and Polaszek, 1996). It is also supported by our observations that some of the parasitoids develop much earlier than others (Table 1) and by observations that virgins females laid male-producing eggs in the already parasitized hosts during the spring. The alternative hypothesis (male-producing egg deposition shortly after female egg deposition), is supported by laboratory observations that male emergence occurs within 3 weeks from shoot samples collection even during the fall and winter. Since male development lasts about 20 days, these male immatures were probably present already when the branches were collected in the field. Unfortunately, we were unable to obtain a full life cycle of the parasitoids on *T. lauri* in the lab, precluding determination of the actual pathway of male production in nature.

4.3. Relevance to biological control

Successful biological control of whiteflies often includes the use of polyphagous parasitoids. One of the latest examples is that of the polyphagous *Encarsia inaron* (Walker) that is found in nature on a range of hosts, including *Aleyrodes singularis* Danzig infesting *lactuca* spp. (Guershon and Gerling, 2001) and the tree pest *Siphoninus phillyreae* Haliday. In 1989 *E. inaron* was introduced into California to control the latter and brought about its complete control (Gerling et al., 2004). Polyphagy is also known in parasitoids used for controlling the invasive *B. tabaci* which is presently controlled

mostly by *Eretmocerus mundus* (Mercet), *E. eremicus* Zolnerowich and Rose and *Encarsia formosa* Gahan of which only the first is relatively host specific. The rapid expansion, biotype speciation and numerous ecological interactions of *B. tabaci* with various host plants (Inbar and Gerling, 2008), require continuous efforts to find new, locally-adapted natural enemies. The success in using non-host-specific parasitoids for control, indicates the usefulness of obtaining biological and ecological information concerning *E. scapeata*, which can then be added to the pool of known *B. tabaci* parasitoids that could be used for its control.

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References

- Anonymous: <http://www.k-state.edu/wgrc/Protocols/Cytogenetics/fixatives.html>.
- Blackburn, M.B., Gelman, D.B., Hu, J.S., 2002. Co-development of *Encarsia formosa* (Hymenoptera: Aphelinidae) and the greenhouse whitefly, *Trialeurodes vaporariorum* (Homoptera: Aleyrodidae): a histological examination. *Archives of Insect Biochemistry and Physiology* 51, 13–26.
- Boivin, G., 1994. Overwintering strategies of egg parasitoids. In: Wajnberg, E., Hassan, S. (Eds.), *Biological Control with Egg Parasitoids*. CAB International, Wallingford, UK, pp. 219–244.
- Brown, J.R., Phillips, J.R., 1990. Diapause in *Microplitis croceipes* (Hymenoptera: Braconidae). *Annals of the Entomological Society of America* 83, 1125–1129.
- Crawley, M.J. (Ed.), 1992. *Natural Enemies*. Blackwell, Oxford.
- Danzig, E.M., 1972. Aleyrodoidea. In: O.L., Danzig, E.M., (Eds.), *Insect and Mite Pests of Agricultural Crops, Part I. Insects Hemimetabola* Krizhanovski, "Nauka" Edition Leningrad, pp. 146–149.
- Erel, E., 2004. Aspects in the biology of the whitefly *Trialeurodes lauri* (Homoptera: Aleyrodidae). M.Sc. thesis, Tel Aviv University, Israel.
- Foltyn, S., Gering, D., 1987. Development and host preference of *Encarsia lutea* (Masi) and interspecific host discrimination with *Eretmocerus mundus* (Mercet) (Hymenoptera: Aphelinidae) Parasitoids of *Bemisia tabaci* (Gennadius), (Homoptera: Aleyrodidae). *Zeitschrift Fur Angewandte Entomologie—Journal of Applied Entomology* 103, 425–433.
- Gelman, D.B., Blackburn, M.B., Hu, J.S., 2002. Timing and ecdysteroid regulation of the molt in last instar greenhouse whiteflies (*Trialeurodes vaporariorum*). *Journal of Insect Physiology* 48, 63–73.
- Gelman, D., Gerling, D., Blackburn, M.B., Hu, J.S., 2005. Host–parasite interactions between whiteflies and their parasitoids. *Archives of Insect Biochemistry and Physiology* 60, 209–222.
- Gerling, D., 1990. Natural enemies of whiteflies predators and parasitoids. In: Gerling, D. (Ed.), *Whiteflies their Bionomics, Pest Status and Management*. Intercept Ltd., Andover, UK, pp. 147–186.
- Gerling, D., Rejouan, N., 2004. Age-related pupal defenses against congeneric internequine activity in *Encarsia* species. *Entomologia Experimentalis et Applicata* 110, 87–93.
- Gerling, D., Alomar, O., Arno, J., 2001. Biological control of *Bemisia tabaci* using predators and parasitoids. *Crop Protection* 20, 779–799.
- Gerling, D., Rottenberg, O., Bellows, T.S.J., 2004. Role of natural enemies and other factors in the dynamics of field populations of the whitefly *Siphoninus phillyreae* (Haliday) in introduced and native environments. *Biological Control* 31, 199–209.
- Godfray, H.C.J., 1994. *Parasitoids: Behavioural and Evolutionary Ecology*. Princeton University Press, Princeton, NJ.
- Guershon, M., Gerling, D., 2001. Parental care in the whitefly *Aleyrodes singularis*. *Ecological Entomology* 26, 467–472.
- Hunter, M.S., Kelly, S.E., 1998. Hyperparasitism by an exotic autoparasitoid: secondary host selection and the window of vulnerability of conspecific and native heterospecific hosts. *Entomologia Experimentalis Et Applicata*. 89, 249–259.
- Hunter, M.S., Woolley, J.B., 2001. Evolution and behavioral ecology of heteronomous. Aphelinid parasitoids. *Annual Review of Entomology* 46, 251–290.
- Inbar, M., Gerling, D., 2008. Plant-mediated interactions between whiteflies, herbivores and natural enemies. *Annual Review of Entomology* 53, 431–448.
- Jervis, M.A., Kidd, N.A.C., 1986. Host-feeding strategies in Hymenopteran parasitoids. *Biological Reviews Cambridge Philosophical Society* 61, 395–434.
- Mehrnejad, M.R., Copland, M., 2005. Diapause strategy in the parasitoid *Psyllaphagus pistaciae*. *Entomologia Experimentalis Et Applicata* 116, 109–114.

- Milonas, P.G., Savopoulou-Soultani, M., 2000. Diapause induction and termination in the parasitoid *Colpoclypeus florus* (Hymenoptera: Eulophidae): role of photoperiod and temperature. *Annals of the Entomological Society of America* 93, 512–518.
- Nichols, J.R., Tauber, M.J., Helgesen, R.G., 1980. Environmental control of diapause and postdiapause development in *Tetrastichus julis* (Hymenoptera: Eulophidae), a parasite of the cereal leaf beetle, *Oulema melanopus* (Coleoptera: Chrysomelidae). *Canadian Entomologist* 112, 1277–1284.
- Onillon, J.C., 1990. The use of natural enemies for the biological control of whiteflies. In: Gerling, D. (Ed.), *Whiteflies: their Bionomics, Pest Status, and Management*. Andover, Intercept, pp. 287–324.
- Pedata, P.A., Hunter, M.S., 1996. Secondary host choice by the autoparasitoid *Encarsia pergandiella*. *Entomologia Experimentalis Et Applicata* 81, 207–214.
- Polgár, L.A., Hardie, J., 2000. Diapause induction in aphid parasitoids. *Entomologia Experimentalis Et Applicata* 97, 21–27.
- Schoonhoven, L.M., Jermy, T., van Loon J.J.A., 1998. *Insect-Plant Biology*. Chapman and Hall.
- Sokal, R.R., Rohlf, F.J., 1981. *Biometry*. Freeman and Co, New York.
- Williams, T., Polaszek, A., 1996. A re-examination of host relations in the Aphelinidae (Hymenoptera: Chalcidoidea). *Biological Journal of the Linnaean Society* 57, 35–45.