



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

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ARTICLE INFO

Article history:

Received 12 December 2007

Accepted 6 February 2009

Available online 20 February 2009

Keywords:

Parasitoids

Encarsia

Whiteflies

Aleyrodidae

Diapause

Arbutus

Monophagy

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. drachne* 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

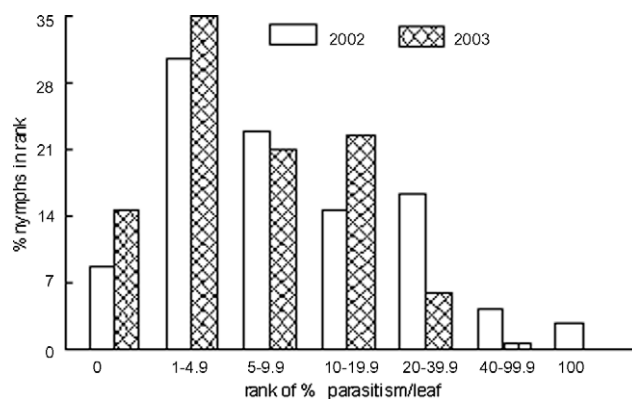


Fig. 1. Frequency distribution of field parasitoid emergence rates of *T. lauri* by *E. scapeata* in 2002 and 2003 ($N = 319$), ranked by density groups per leaf.

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