Observations of the Biologies and Interrelationships of Parasites Attacking the Greenhouse Whitefly, *Trialeurodes vaporariorum* (West.), in Hawaii[1]

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ABSTRACT

Prospaltella transvena, Eretmocerus nr. *haldemani, Encarsia formosa* and *Aleurodophilus pergandiellus* were recovered as parasites of *Trialeurodes vaporariorum* on *Sonchus oleraceus* and *Emilia* spp. on Oahu between January and May 1980. Parsitization often was close to 100%. The first three parasite species were relatively abundant; the last was rare. High parasitization was probably one factor limiting whitefly infestations on these plant species. Multiple parasitism involving *Encarsia* type parasites and *Eretmocerus* was frequent, probably because the latter lays eggs externally and the former, internally. Superparasitism by *Eretmocerus* was rare. Superparasitism by the *"Encarsia* type" parasites *(Encarsia, Aleurodophilus* and *Prospaltella)* was more frequent, but was indistinguishable, in part, from male hyperparasitism.

The greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood) (Homoptera: Aleyrodidae), is a polyphagous, cosmopolitan species (Mound and Halsey 1978). In the tropics and subtropics it is mainly a pest of outdoor crops, whereas in cooler climates it may damage greenhouse-grown vegetables and flowers (Hussey, Read and Hesling 1969).

T. vaporariorum was probably introduced into Hawaii before 1900 and has been recorded as a pest of beans for many years (Zimmerman 1948, Sherman and Tamashiro 1957). It has several species of natural enemies in Hawaii, including the following parasite species: *Prospaltella transvena* Timberlake, *Eretmocerus* nr. *haldemani* Howard, *Encarsia formosa* Gahan and *Aleurodophilus pergandiellus* (Howard).

During the months of Jan.-May 1980 I had the opportunity to observe populations of *T. vaporariorum* in Hawaii. Bearing in mind that only meager biological information on *P. transvena* existed and that no studies had been done on the interrelationships of the parasite species under Hawaiian conditions, I tried to determine the life cycle of *P. transvena.* I also tried to determine the abundance of the whitefly and its introduced parasites on wild plants and, where possible, to get an indication of their effectiveness. Finally, an attempt was made to elucidate the interrelationships among the parasite species.

MATERIALS AND METHODS

All work was done with greenhouse whiteflies using *Sonchus oleraceus* L. and *Emilia* spp. as host plants. Most of the insects were collected on the campus of the University of Hawaii at Manoa. Additional material was obtained in the University of Hawaii Experimental Farm at Waimanalo on the windward side of Oahu, and near Kapiolani Blvd. in the vicinity of the Ala Moana Shopping Center in Honolulu. All plants were growing wild and received no pesticide applications.

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The distribution of whiteflies on the plants was examined by picking 39 whitefly-infected plants, counting the leaves on each plant, and sorting them into 3 categories: Clean = no whiteflies, low = up to 25, and heavy = above 25 whitefly third and fourth instar nymphs and pupae per leaf.

Rearing took place in a greenhouse, within parasite-free screen cages. Infested leaves were taken from the cages and used for the various experiments. The leaves were detached and placed on a moist filter paper within a plastic petri-dish. Whole plants or leaves were also enclosed in organdy bags and used thus.

Data on parasite ovipositional preferences were obtained by observing behavior of female parasites in the laboratory. Field parasitization data were obtained by placing immature, parasitized and unparasitized whiteflies individually in glass vials and observing the emergence of adults. Interrelationships between the parasites under field conditions were determined through dissections of 18 field-collected leaf samples containing parasitized whiteflies. Dissections were also used to follow the development of immature parasites.

In mating experiments, males were placed in glass vials with parasitized whitefly pupae from which females of the same parasite species were about to emerge. As soon as the females had emerged and mated they were either dissected for examination of the spermatheca, using a phase-contrast microscope, or were allowed to oviposit in whitefly pupae.

All rearing and life cycle studies were carried out under room conditions of natural external day length and temperatures of 24-26°C.

RESULTS

The host plants and *T. vaporariorum* were found readily throughout Oahu. Infestations were heavy at times, but sporadic. Whitefly abundance on host leaves, as determined from counts from 39 *S. oleraceus* plants having 10.18 + 0.5 (mean + S.E.) leaves per plant, was: Clean 26.4%, low 38.8%, and high 34.7%.

Prospaltella transvena **Timberlake.**

Mated *P. transvena* females were found mainly on leaves containing young whitefly nymphs. Development from oviposition to emergence took 15 days. As in the other whitefly parasites, the host pupated before it was killed and devoured. *P. transvena* pupated within a black pupal skin that was readily visible through the transparent whitefly puparium. The emerging adults were entirely yellow. Like many other congenerics, the males developed as secondary parasites on females of their own species, or of *E. formosa* or *E.* nr. *haldemani.* A virgin female was also observed depositing an egg upon an unparasitized whitefly pupa. However, confining additional virgins with more such pupae failed to yield parasite progeny.

Being external parasites, the males of *P. transvena* have open spiracles from the first instar on. Consequently, male producing eggs are always laid in a dry environment, i.e. on hosts that have finished devouring the whitefly and are about to pupate or have already pupated. Oviposition of male eggs may take place on nearly mature hosts, as evidenced by the fact that I found an *E.* nr. *haldemani* female that had already gnawed an emergence hole from the whitefly puparium, but was dying because a first instar male larva was feeding on its abdomen.

Mating occurs shortly after emergence; therefore, mated females were obtained by confining males with female pupae which were ready to emerge. However, I was occasionally successful in obtaining mated females by confining older individuals with males in glass vials. The sex ratio in the field favors females greatly. No large statistically significant population counts were made, but in the field collected material I often got no males, or ratios as low as 1:33. Yet, all field collected adult females that were examined had full spermathecae.

P. transvena adults feed on the honeydew of the whiteflies, and were observed to imbibe from exuviae of emerged whiteflies as well as from larvae. Females also host feed. As in other species, this is preceded by the insertion of the ovipositor into the host. In my observations, virgin females drilled and fed on 2nd instar nymphs as well as on mature whitefly pupae that were almost ready to emerge. An unmated female was seen feeding upon a whitefly pupa and then laying an egg on its thorax. I did not observe mated females host feeding.

***Encarsia formosa* Gahan**

This cosmopolitan species is used widely for the control of the greenhouse whitefly, especially in glasshouses, and has been the subject of numerous biological and ecological studies (Burnett 1962; Gerling 1966a; Lenteren et al. 1976; Nechols and Tauber 1977; Scopes 1969 and many others). *E. formosa* was introduced from Canada to Hawaii in 1948 (Swezey 1949) and is usually abundant wherever the host occurs.

The life cycle from egg to adult was 15 days. *E. formosa* is usually parthenogenetic, males being extremely rare. Burnett (personal communication) and Gerling (1966a) found them only under laboratory conditions of very high parasitization, and the latter determined that they developed as parasites of the females. During the present study 11 males were recovered from field collected material. These emerged from black host puparia and from transparent ones. The former probably housed *E. formosa* females whereas the latter contained remnants of *P. transvena*. Attempts to obtain copulation of these males with emerging *E. formosa* females failed.

***Aleurodophilus pergandiellus* (Howard) (formerly *Encarsia pergandiella* Howard)**

Only 1 female, 1 pupa and possibly a few eggs of this species were encountered during this study. The biology of *A. pergandiellus*, as known from the literature (Gerling 1966b), resembles that of *E. formosa*, differing mainly in the facts that *A. pergandiellus* is biparental and that no blackening of the host puparium occurs.

***Eretmocerus* nr. *haldemani* Howard**

This *Eretmocerus* was introduced into Hawaii from California for control of the greenhouse whitefly. There, what is probably the same species has been referred to as *E. californicus* (Gerling 1966c), and later, following a study of material at the U.S. National Museum, as *E. haldemani* (Gerling 1967). Following additional biological and taxonomic investigations, I feel that, for the present, it is not advisable to affix a definite specific name to this insect. Therefore, the name *E.* nr. *haldemani* is being used.

Other parasite species

In addition to the 4 species mentioned, occasional unidentified egg-like objects were found in the dissections. These did not conform with the shapes of the known parasite eggs. Also, on 1 occasion, 5 first instar larvae of what appeared to be an unrecognized hyperparasitic male were found.

Host and parasite interactions

Examination of the samples of infested leaves revealed high percentage of parasitism (Table 1). A breakdown of the parasite fauna according to the results of dissections of the whiteflies found upon 18 of the 35 leaves in Table 1 revealed the almost ubiquitous occurrence of *Eretmocerus*, *Encarsia* and *Prospaltella* species, as well as high incidence of both multiple and superparasitism (Table 2). Table 2 also shows that predominance of parasite species was not uniform throughout the samples. In Manoa, I usually found either *E.* nr. *haldemani* or *P. transvena* dominant, wtih *E. formosa* also contributing measurably. Whiteflies on the leaves of *S. oleraceus* and *Emilia* spp. around Ala Moana, in a much drier area, were parasitized predominantly by *E. formosa* (Table 2 Nos. 4-6) with some individuals of the 2 other species also being present. In contrast, material from Waimanalo, on the rainy, windward side of Oahu, contained *T. transvena* almost exclusively (Table 2 Nos. 1-3).

All of the parasite species discussed are obligatorily solitary, yet more than one parasite individual was often found within a single host. These multiple ovipositions were both intraspecific (superparasitism) and interspecific (multiple parasitism) (Tables 2 and 3).

Only 2.5% (n = 200) of the hosts attacked by *E. haldemani* were superparasitized. Of the *Encarsia* type parasites (= *Encarsia, Aleurodophilus* and *Prospaltella),* 30% (n = 130) showed evidence of multiple ovipositions. These included super- and multiple parasitism among the 2 species, and were confined to the eggs and 2 first larval instars. In 4 cases in which eggs were deposited upon 1st instar parasite larvae, all of the organisms involved died. In the others, one or both survived, at least until the end of the second instar (Table 3).

Correlation tests were run between percent superparasitism and percent of "*Encarsia* type" single parasitizations, and between the former and total percentage of parasitized whiteflies. Both were low and insignificant (r = 0.318 and 0.360 respectively). However, a significant negative correlation was found between percent superparasitism of "*Encarsia* type" and percent parasitization by *Eretmocerus* (r = -0.629, $p < 0.05$).

Multiple, interspecific parasitization involving *E.* nr. *haldemani* and the *Encarsia-Prospaltella* complex was commmon. Most of the cases involved eggs, and the first 2 larval instars of all parasite species. The *Eretmocerus* always survived these encounters.

One case of an *Eretmocerus* prepupa occupying the same host as an *Encarsia* type third instar larva was found. Also, 14 *Eretmocerus* pupae were subjected in the laboratory to parasitization by *P. transvena* virgins and dissected at various intervals thereafter. The progeny of the latter survived in all of the cases (Table 3). Correlation between percentage of multiple parasitism and that of total parasitism was low and insignificant (r = 0.482), as was the correlation of multiple parasitism with the percentage of occurrence of *Eretmocerus* within the dissections (r = -0.22).

DISCUSSION

The limited field data available indicate that each of the 3 principal parasite species alone is capable of reaching a very high degree of parasitization. It is apparent that the species ratio of the parasite complex occurring on a particular leaf is determined by ecological conditions, and by success of each species in reaching the particular leaf in question.

The parasite complex of the greenhouse whitefly in Hawaii is a unique conglomerate of species, derived from both the Old and the New Worlds. *P. transvena* is known as a parasite of *Singhius hibisci* (Kotinsky) (Timberlake 1926), a whitefly that occurs in the Far East as well as Hawaii (Mound and Halsey 1978). It probably adopted *T. vaporariorum,* which is of American origin, as a host in Hawaii.

E. formosa was introduced into Hawaii from Canada and *A. pergandiellus* was brought from California, both to combat *T. vaporariorum.* An apparently stable balance of the whiteflies has been obtained on wild populations on *S. oleraceus* and *Emilia* spp., whereby only about ⅓ of the leaves are heavily infested and parasitization is usually very high, precluding severe outbreaks of the pest. However, commercial crops such as beans (Sherman & Tamashiro 1957) or greenhouse crops (personal observation) are sometimes severely affected.

Biologically, the parasites exhibit two distinct developmental modes; thelytoky, in which the females reproduce by parthenogenesis as in *Eretmocerus* and *E. formosa*, and autoparasitic (adelphoparasitic) arrhenotoky, in which the haploid males develop as parasites of the diploid females (Flanders 1937, Viggiani 1981). Males of *Encarsia, Aleurodophilus* and *Prospaltella* may also develop hyperparasitically upon various other whitefly parasites. The latter mode was exhibited mainly by *P. transvena* and the rarely found *A. pergandiellus. E. formosa* constitutes a special case because it is commonly thelytokous. However, occasional males, which in the past were known to show up only under laboratory conditions of extemely heavy parasitization, were probably the product of autoparasitism (Gerling 1966a). Eleven such males were recovered in Hawaii from field collected material. A possible explanation is the fact that the rate of parasitization was often so high that the *E. formosa* females were unable to find unparasitized hosts suitable for normal female development, and reverted to parasitizing either their own larvae or those of other whitefly parasites.

The biological differences between the species also underlie their behavior when encountering parasitized hosts, and hence the results of such encounters. When considering the behavior of a female one must differenctiate between her ability to recognize that the host has already been parasitized and her reaction to this situation.

The scarcity of superparasitism by *Eretmocerus* indicates that this species usually recognizes hosts that have been parasitized by conspecifics. The high rate of multiple parasitism of *E.* nr. *haldemani* and the *"Encarsia* type" parasites, on the other hand, can be explained by the fact that although both species accept the same host instar for oviposition, the former oviposits under the host and the latter, within it.

The abundance of supernumerary parasitization by the *"Encarsia* type" females (Table 3) is more difficult to explain. It might be attributed in part to a lack of recognition of already present eggs on young larvae; to the autoparasitic habit of the females, as attested by the occurrence of *E. formosa* males, and by the scarcity of unparasitized hosts. The latter point is supported by the observation that in spite of the overall lack of correlation between percent parasitism and superparasitism ($r = 0.360$) the higher rates of superparasitism occurred on leaves on which percentage parasitism by *"Encarsia* type" parasites was usually high (Tables 1 and 2, Nos. 9-11).

The decrease in percent superparasitism by *"Encarsia* type" parasites with the increase of percent parasitization by *Eretmocerus* as indicated by the negative correlation cannot be explained due to the small sample at hand. However, it may indicate some recognition of whiteflies already parasitized by *Eretmocerus* by the searching *Encarsia* females, and an associated change of behavior.

The fate of the parasite progeny under condition of supernumerary oviposition varies. Whenever a larva of *Eretmocerus* is present, the *"Encarsia* type" larva dies. This may be due to a humoral substance, since the 2nd and 3rd instars of *Eretmocerus* have recessed mandibles (Gerling 1966c). It is noteworthy that 2 *Eretmocerus* larvae of the 2nd instar were found alive in the same host (Table 3).

A different fate awaits *E.* nr. *haldemani* when its more developed instars are encountered by an *"Encarsia* type" female. If the latter has mated, it may act as a hyperparasite of the 3rd instar *Eretmocerus* larva, depositing an egg within it. If unmated, the *P. transvena* female may deposit a male producing egg externally on the

Eretmocerus, provided the latter has finished feeding upon its host and is in a dry environment.

Interactions of *"Encarsia* type" progeny with each other do not seem to show a regular pattern as to the victor in the competition. However, in some cases the supernumerary eggs or first instar larvae die, whereas in other hosts the second and third instar larvae were found alive side by side. It must be mentioned that part of these supernumerary immatures, especially the ones associated with more developed progeny within the whiteflies, were probably males that were destined to develop as hyperparasites.

TABLE 1. Parasitization of *T. vaporariorum* on leaves of *S. oleraceus.*

Leaf No.	No. of whiteflies per leaf	% parasitization
1	22	13.6
2	8	100.0
3	23	65.9
4	40	97.5
5	63	95.2
6	70	94.2
7	11	36.3
8	12	75.0
9	10	100.0
10	13	92.3
11	14	85.7
12	22	59.1
13	19	89.4
14	26	73.1
15	39	84.6
16	38	89.4
17	38	100.0
18	164	91.3
19	82	80.5
20	35	97.1
21	73	89.0
22	44	93.2
23	76	85.5
24	67	95.5
25	45	86.6
26	20	100.0
27	15	100.0
28	22	95.5
29	8	62.5
30	12	100.0
31	17	100.0
32	20	80.0
33	20	95.0
34	15	100.0
35	22	68.2
Mean		87.5

TABLE 2. Breakdown of parasitism of *T. vaporariorum* samples Nos. (1-18) according to the species involved (dissections), Oahu, Hawaii, Feb-May, 1980.

Leaf No.	No. of parasitized whiteflies	Total % parasitism	% *Eretmocerus*	% *E. formosa* or *E. transvena*	% Multiple parasitism (1+2)	% Super parasitism	Unidentified parasites
(W)1	3	13.6	0.0	100.0[c]	0.0	0.0	
(W)2	8	100.0	0.0	62.5[c]	0.0	37.5	
(W)3	16	65.9	0.0	87.5[c]	12.5	0.0	
(A)4	39	97.5	0.0	97.5[b]	0.0	0.0	
(A)5	60	95.2	33.3	17.4[c], 39.7[b]	0.0	4.8	
(A)6	66	94.2	15.7	20.0[c], 44.2[b]	0.0	12.8	1
7	4	36.3	25.0	75.0[a]	0.0	0.0	
8	9	75.0	22.2	55.5[a]	0.0	22.2	
9	10	100.0	10.0	10.0[a]	20.0	60.0	
10	12	92.3	8.3	16.6[a]	25.0	41.6	1
11	12	85.7	16.6	33.3[a]	8.3	41.6	
12	13	59.1	61.5	23.1[a]	7.7	7.7	
13	17	89.1	52.9	23.5[a]	17.6	5.8	
14	19	73.1	0.0	84.1[a]	0.0	15.8	
15	33	84.6	57.5	27.2[a]	6.0	9.0	
16	34	89.4	35.3	20.6[a]	35.3	8.8	
17	38	100.0	50.0	15.7[a]	23.7	10.4	
18	150	91.3	84.0	6.0[a]	1.3	6.1	2

(W) = collected in Waimanalo.
(A) = collected in vicinity of Ala Moana.
Unmarked = collected in Manoa.
[a]Either one or both, specific identity not clear.
[b]*E. formosa.*
[c]*P. transvena.*

TABLE 3. A classification of the instances in which more than one individual parasite was found within the same whitefly host, enumerating the numbers of such instances and their outcomes.

1. All parasites of the *"Encarsia* type".

No. of cases	*Findings*
2	2 living eggs
4	1 dead egg and 1 dead LI
3	1 dead egg and 1 living LI
2	2 living eggs and 1 living LI
1	1 living LI and 1 dead LI
3	1 living egg and 1 living LII
1	1 living egg and 1 dead LII
1	1 living LII and 1 dead LI
1	1 living LII and 1 dead LII
1	1 living egg and 1 living LIII
1	1 dead egg and 1 living LIII
1	1 living LI and 1 living LIII
3	1 living LII and 1 living LIII
4	1 living egg and 1 living prepupa
2	1 living larva I and 1 living prepupa

2. Multiple parasitism, *"Encarsia* type" and *Eretmocerus* found on or in same host individual.

No. of cases	*Findings*
1	1 living *Er.* egg and 1 living *Enc.* egg
1	1 living *Er.* egg, 1 living *Enc.* egg and 1 dead *Enc.* LI
3	1 living *Er.* egg and 1 living *Enc.* LIII
2	1 living *Er.* egg, 1 living *Enc.* egg, 1 living *Enc.* LIII
1	1 living *Er.* egg, 1 living *Enc.* prepupa
1	1 dead *Er.* egg, 1 living *Enc.* LII
2	1 living *Er.* egg, 1 living *Enc.* LII
3	1 living *Er.* LII, 1 dead *Enc.* LI
2	1 living *Er.* LII, 1 living *Enc.* egg, 1 dead *Enc.* egg
2	1 living *Er.* LII, 1 living *Enc.* LII
7	1 living *Er.* LII, 1 dead *Enc.* LII
2	1 living *Er.* LII, 1 dead *Enc.* LIII
1	1 dead *Er.* prepupa, 1 living *Enc.* LIII
*3	1 living *Er.* pupa, 1 living *Enc.* egg
*2	1 dead *Er.* pupa, 1 living *Enc.* LII
*8	1 dead *Er.* pupa, 1 living *Enc.* LIII
*1	1 dead *Er.* pupa, 1 living *Enc.* pupa

3. Both parasites *Eretmocerus.*

No. of cases	*Findings*
2	2 living eggs
2	1 living egg, 1 living LII
1	1 living egg, 1 living LII, 1 dead *Enc.* LII

All *Eretmocrus* eggs and 1st instar larvae were mentioned together, as eggs.
Er. = *Eretmocerus, Enc.* = *Encarsia.*
LI, LII, LIII = Three larval instars of the parasites.
*4 last cases of multiple parasitism were obtained in the laboratory.

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