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Quantitative Evaluation of Natural Enemy Impact Against the Homopteran Pests of Citrus

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C. Abstract

The Israel group studied several aspects of natural enemy responses and interactions:

I) Interactions between different species attacking the same host. 1. Aphytis holoxanthus DeBach and Pteroptrix smithi (Compere) (Hymenoptera: Aphelinidae) attacking the Florida red scale, Chrysomphalus aonidum (L.) (Homoptera: Diaspididae; 2. Aphytis species- A. melinus DeBach and A. chrysomphali (Mercet) and Comperiella bifasciata Howard (Hymenoptera: Encyrtidae), attacking the California red scale, Aonidiella aurantii (Maskell) (Homoptera: Diaspididae). II) A comparative study of two species of predatory ladybeetles of the genus Chilocorus (Coleoptera: Coccinellidae): C. bipustulatus (L.), an endemic species, and the newly imported C. kuwanae Silvestri. III) Population dynamics of the Florida wax scale, Ceroplastes floridensis Comstock (Homoptera: Coccidae), and its natural enemies. The main parasites attacking this important pest of citrus were found incapable of regulating its populations in Israel.

The California group sought to understand why a natural enemy, A. melinus, regulated a pest scale-insect, the California red scale, at subeconomic densities in parts of the scale insect's range and not in others. Some of the attributes suggested as characterizing a successful biological control agent were tested with this system, and most of them were found inadequate in predicting the natural enemy's success or failure. Instead, two factors appear important in the success of A. melinus as biological control agent: 1. It requires a certain minimal host size for daughters production, whereas smaller scale insects receive male parasitoid eggs. 2. The abundance of the appropriate host size required for parasitoid daughters varies seasonally and geographically: the further inland the location, the more variable the abundance. In San Joaquin Valley, the appropriate scale stages are absent or scarce during extended periods, hence few female natural enemies are produced to control the greater abundance of this stage subsequently. We hypothesize that winter temperature patterns produce this variation in the abundance of appropriate hosts.

**Quantitative Evaluation of Natural Enemy Impact Against the Homopteran
Pests of Citrus.**

by

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INTRODUCTION

Biological control is a widely practiced means of pest management, which has had a long successful history in association with citrus. Moreover, biological control of certain pests has been the foundation for the development of integrated pest management on citrus. Yet, in spite of its widespread application, this control technique is still largely ad-hoc in approach. The attributes which define a desired biological control agent have been speculated upon or theoretically determined, but only a few empirical studies have attempted to explore these speculations. It was the purpose of our research to use a comparative behavioral approach to explore some of the attributes which make a natural enemy an effective biological control agent, and to study the interspecific interactions in the citrus agroecosystem in cases where more than a single parasite (or predator) species attacks a common host.

This Final Report is composed of two separate sections, one presenting the research carried out by the Israeli group, the other describing the California portion of the study.

SECTION 1: Research in Israel

The Israeli group studied several aspects of natural enemy responses and interactions:

I) Interactions between different species attacking the same host. This was studied with the parasite complexes attacking two major pests of citrus: 1. Aphytis holoxanthus DeBach (Hymenoptera: Aphelinidae), an external, facultatively gregarious parasite, and Pteroptrix smithi (Compere) (Hymenoptera: Aphelinidae), an internal gregarious parasite, both attacking the Florida red scale, Chrysomphalus aonidum (L.) (Homoptera: Diaspididae); 2. Aphytis species - A. melinus DeBach and A. chrysomphali (Mercet) - external, facultatively gregarious parasites, and Comperiella bifasciata Howard (Hymenoptera: Encyrtidae), an internal solitary parasite, attacking the California red scale, Aonidiella aurantii (Maskell) (Homoptera: Diaspididae).

II) A comparative study of two species of predatory ladybeetles of the genus Chilocorus (Coleoptera: Coccinellidae): C. bipustulatus (L.), an endemic species, and C. kuwanae Silvestri, a newly imported species which was being mass reared and colonized in Israel during the period of this study.

III) Population dynamics of the Florida wax scale, Ceroplastes floridensis Comstock (Homoptera: Coccidae), and its natural enemies. An attempt was made to evaluate the contribution of natural enemies to changes in the population density of this important pest of citrus. Several manuscripts, summarizing the main findings of this project, are now being prepared for publication.

I. Interactions between parasite species attacking the same host.

1. Aphytis holoxanthus DeBach and Pteroptrix smithi (Compere), parasites of the Florida red scale in Israel: a comparative study.

This system, comprising parasites of two different aphelinid genera parasitizing the same host, was selected for this study because of its interesting history in Israel. Both species were simultaneously

introduced into Israel during the 1950's and the course of their establishment has been rather well documented. A total of 70 airmail shipments were received from Hong Kong during 1956-57 (Rosen & DeBach 1979). However, although both species were released simultaneously in citrus groves around Rehovot, their subsequent performance was entirely different. A. holoxanthus increased very rapidly and reduced the Florida red scale to subeconomic levels within 2-3 years. P. smithi, on the other hand, was not recovered from field samples until 1960, and even by 1964 was found to be established only in the Rehovot area (Rosen 1965, Rivnay 1968). It then began slowly to disperse and increase in residual host populations along the coastal plain, and later also in other citrus regions in Israel (e.g., Porath 1969). This very gradual increase in P. smithi was followed by a marked decrease in parasitism by A. holoxanthus. The research reported herein was intended to determine the current relative abundance of these species, and to explain the changes that have taken place during the last 20 years or so, in view of their response and interaction under controlled conditions.

The current situation in citrus groves

METHODS

Two study plots, both located in the coastal plain of Israel, were selected for this study: Shefayim - Shamouti oranges grafted on sweet lime and inarched with sour oranges, planted in 1962. Gan-Efrayim - Shamouti and Valencia oranges, grafted on sweet lime and on sweet lime inarched with sour orange, respectively, planted in 1952.

Three randomly selected rows in each plot served as sampling rows throughout the study period. Samples were taken monthly and comprised 100-200 scale-infested leaves and 20-30 infested fruits per row. The samples were brought to the laboratory and the scales were dissected under a stereoscopic microscope and checked for active parasitism, i.e., for presence of live developmental stages of parasites.

RESULTS

The Shefayim plot was sampled from September 1980 until August 1981. The results are presented in Fig. 1. Inasmuch as the location of the sampling row was found to have a significant effect on the rates of parasitism by the two species, the results for the row near the margin of the grove are presented separately from the inner rows.

Figure 1. Rates of parasitism of the Florida red scale by ( ) *Aphytis holoxanthus* and ( ) *Pteroptrix smithi* on fruits and leaves in Shefayim during 1980-81. The values on top present the number of scale insects examined. The left bar in each pair represents the marginal row and the right bar represents the inner row. The values in parentheses present the number of treatments against the Medfly.

Total parasitism exceeded 50% during most of the sampling period, reaching 80 and 90% on fruit in December and April, respectively, and 90, 88 and 100% on leaves in October, April and May, respectively. *A. holoxanthus* reached higher proportions on leaves in the marginal row (up to 44% in November) than in the inner rows (not exceeding 18% in spring). The population of *P. smithi* on leaves was usually higher and more stable. In the marginal row it fluctuated between 31 and 64%, and

in the inner row between 39 and 81%. Parasitism by A. holoxanthus on fruit was also lower than that of P. smithi.

In Gan-Efrayim there was no difference between the rows, so the data presented in Fig. 2 are pooled. Total parasitism was ca. 50% on leaves during winter, and exceeded 90% in August. A similar trend was observed on fruits (up to 98% in spring on fruits that were not picked). Again, P. smithi was the dominant species, and its rate of parasitism was significantly higher than that of A. holoxanthus. In fact, parasitism by A. holoxanthus on fruits was so extremely low that it could practically be ignored.

Other natural enemies of the Florida red scale were negligible throughout the study period. However, parasitism by the two species under study was sufficient to maintain the pest below the economic threshold.

Figure 2. Rates of parasitism of the Florida red scale by () Aphytis holoxanthus and () Pteroptrix smithi on A. leaves and B. fruits in Gan Efrayim during 1980-82. Values on top present the number of scale insects examined. The values in parentheses present the number of treatments against the Medfly.

These data are in good agreement with the trends reported previously, that P. smithi has become the dominant parasite, whereas the population of A. holoxanthus has decreased.

In the following sections, we attempt to elucidate the biological and ecological background underlying these phenomena.

Interspecific host discrimination and intrinsic competition between A. holoxanthus and P. smithi

Interspecific competition between two or more species of parasites attacking the same host involves two aspects: extrinsic competition, i.e., competition between adult parasites through their searching capacity and host discrimination ability, and intrinsic competition between developing larvae upon, or inside, an individual host (Flanders 1966, Rosen & Huffaker 1983). Host discrimination and intrinsic competition between Aphytis and Pteroptrix have been studied in the field and in laboratory experiments. Their role in the interspecific relationships between these parasites will be discussed in the following sections.

Host discrimination: Host discrimination is the ability of an insect parasitoid to avoid attacking, or accepting, a potential host that has already been parasitized (Vinson 1976). Various authors have investigated cases of host discrimination in relation to intraspecific as well as to interspecific competition (e.g., Force & Messenger 1965, Wylie 1970, 1971, 1972a, Vinson 1972, Weseloh 1983).

Quantitative evaluation of host discrimination was usually carried out by either direct observation of parasite searching and ovipositional behavior, or by analysis of parasite egg distribution. The former method included description of the behavioral sequence leading to oviposition (Force & Messenger 1965, Wylie 1970, 1972a, Weseloh 1983) and recording the time allocated for this process (Price 1970, Wylie 1971, Vinson 1972). The latter method involved examining the extent of deviation of egg distribution by the parasite from the Poisson model for random distribution.

Host discrimination may involve either secretion of marking semiochemicals by the female parasite on the searched substrate (Price 1970, Vinson 1972) or on the external surface of the host (Flanders 1951, Vinson 1972, Weseloh 1976, Podoler & Mendel 1977, Bosque & Rabinovich 1979), or injection of venom into the host's body (Wylie 1970, 1971, 1972a), causing certain changes in its haemolymph (Ganesalingam 1974). External marking may be detected by both the antennae and the ovipositor of the female parasite, whereas internal marking can be detected only by the ovipositor. Both external and internal marking may occur in sessile hosts, whereas internal marking is the major mode in mobile ones (van Lenteren et al. 1978).

Intrinsic competition: Intrinsic competition between insect parasites may occur in solitary as well as in gregarious species, in endo- as well as in ectoparasites. It may be intraspecific (in superparasitism) as well as interspecific (in multiparasitism).

Based on his observations of solitary endoparasites, Salt (1961) suggested that larvae of parasitic Hymenoptera can eliminate their competitors by (1) internal physical attack, (2) physiological suppression, (3) random attack, or (4) selective starvation. The fact that the larvae of Aphytis and Petroptrix inhabit the host externally and internally, respectively, reduces the possibility of direct physical contact between them. Physiological suppression and starvation therefore appear to be the most likely mechanisms of elimination. Another significant factor affecting the outcome of intrinsic competition is the rate of egg and larval development of the competing species (Wylie 1972b).

MATERIALS AND METHODS

Florida red scale, reared on lemon fruits, served as host for the parasites.

The parasites were confined in experimental units consisting of plastic vials (3.2cm in diameter and 2.5cm high), which were glued to the lemon with plastic glue. Fine-mesh netting, fitted with a rubber

band, served as cover. For direct observations, a 4x4cm glass plate was fitted to the vial with cello tape. Honey-soaked strips of paper (1.5 x 0.5cm) were placed on the walls of the vial to provide the parasites with food.

Each unit contained ca. 20 hosts. Four female parasites of a given species, up to 48h in age, were introduced into a unit, and their ovipositional behavior was observed for ca. 3h under a stereoscopic microscope. The parasites were then removed with a fine brush. A host was considered parasitized only when complete ovipositional behavior was observed (for Aphytis - as described by Rosen & DeBach 1979, and for Pteroptrix - as described by Bar & Gerling 1971).

To study interspecific host discrimination, the hosts were first exposed to one species, and those parasitized in each unit (usually 4-10 per unit) were recorded. Females of the other species were then introduced, and their behavior was observed. This was done at different intervals after the first species had been removed, in order to determine the ability of the second species to detect hosts containing eggs, young larvae (L1) or mature larvae (L2+L3) of the first. In accordance with their rates of development, these intervals were 0, 2, and 5 days when Pteroptrix followed Aphytis, and 0, 6, and 10 days when Aphytis followed Pteroptrix. The scale insect hosts parasitized by the second species were recorded, and 2-10 days later they were dissected and the parasites developing in them were identified. Multiparasitized hosts provided the data for analysing intrinsic competition. All experiments were conducted under conditions of $27\pm1^{\circ}\text{C}$ and RH $70\pm5\%$, and a photoperiod of 16L:8D.

RESULTS AND DISCUSSION

Host discrimination: Aphytis appears to be capable of detecting hosts parasitized by Pteroptrix (Table 1), but the results of discrimination depend on the age of the latter. When exposed to hosts containing eggs of Pteroptrix, Aphytis attacked a significantly higher proportion of parasitized than unparasitized hosts. With hosts containing young larvae of Pteroptrix, it attacked an equal proportion

of parasitized and unparasitized ones, but when exposed to hosts containing mature larvae, it attacked a significantly lower proportion of parasitized ones.

Table 1. The ability of A. holoxanthus and P. smithi to detect already parasitized hosts.

PARASITE INSTAR	<u>Aphytis</u> following <u>Pteroptrix</u>		<u>Pteroptrix</u> following <u>Aphytis</u>	
	Mean	oviposition	in hosts:	
HOST	Parasitized by <u>P. smithi</u>	Unparasitized	Parasitized by <u>A. holoxanthus</u>	Unparasit.
Egg	52.501	28.987*	45.780	38.325
L1	31.603	37.009	33.805	42.953
L2+L3	14.611	37.607**	0	25.552*

* Difference significant at $P < 0.05$

** Difference significant at $P < 0.02$

By using the ratio between the number of hosts actually multiparasitized by both species (O) and the expected number assuming no discrimination (Ex), (Fig. 3), it can be shown that Aphytis was attracted to hosts containing eggs of Pteroptrix ($O/Ex > 1$).

Pteroptrix, on the other hand, did not appear to detect parasitized hosts containing eggs and young larvae of Aphytis (Table 1), and the O/Ex ratio did not differ from 1.0 (Fig. 3). However, it did detect and avoid parasitized hosts containing mature larvae of Aphytis ($O/Ex < 1$).

The results of these experiments suggest the possible existence of several mechanisms of host discrimination.

Figure 3. Detection by *Aphytis holoxanthus* (●) and *Pteroptrix smithi* (○) of hosts containing developmental stages of the competing species, as expressed by the O/Ex ratio. O, Ex - multiparasitized hosts observed and expected assuming no discrimination, respectively. E - eggs; L - larvae.

In the case of *Aphytis*, attraction to hosts immediately following their parasitization by *Pteroptrix* may indicate that an external marking semiochemical is involved. Host marking, intended to reduce the probability of intraspecific superparasitism, is rather common among the parasitic Hymenoptera (e.g., Vinson 1976). It is conceivable that a volatile marking pheromone of *Pteroptrix* may serve as a kairomone, attracting *Aphytis* to the same hosts. Volatility would explain its short-term effect, attracting *Aphytis* only to hosts containing eggs of *Pteroptrix* but not later stages. On the other hand, attraction of *Aphytis* to a kairomone of the host itself, that had also attracted *Pteroptrix*, would not explain why *Aphytis* did not respond to hosts containing young larvae of *Pteroptrix*, nor why *Pteroptrix* was not attracted to hosts containing *Aphytis* (Quednau & Hubsch 1964, for example, reported the attraction of certain *Aphytis* species to a water-soluble component of the scale cover of armored scale insects).

Avoidance by both Aphytis and Pteroptrix of hosts parasitized by mature larvae of the other species may be mediated by changes in the host, caused by the developing parasite larvae. In the case of Aphytis, it appears that the soft body of a healthy, non-moulting scale insect host, and its movements underneath the scale cover, serve to stimulate oviposition by the parasite (Baker 1976). Females of Aphytis might, therefore, be able to recognize the harder, less mobile parasitized hosts containing mature larvae of Pteroptrix. Similarly, when Pteroptrix was observed drilling into hosts containing mature larvae of Aphytis, subsequent dissection did not reveal any Pteroptrix eggs in them. Hosts parasitized by advanced larvae of Aphytis are noticeably shrivelled, most of the space between the scale cover and the substrate being filled with the ectoparasite's larvae. It is likely that the Pteroptrix female is able to use her ovipositor to distinguish between the body of a healthy host and those of the Aphytis larvae.

In all instances of multiple attack observed in this study, there was no indication of hyperparasitism of Pteroptrix on Aphytis, or vice versa.

Intrinsic competition: All hosts in which multiparasitism was indicated by the parasites' ovipositional behavior, were further examined to follow the development of the parasite larvae. Intrinsic competition usually resulted in one species overcoming and outcompeting the other. The larvae of the winner developed normally, whereas those of the loser remained inactive, deteriorated, and their digestive tract became conspicuously dark (Fig. 4).

The distribution of successes and failures of the two species in intrinsic competition is summarized in Table 2 for the various combinations described above. The values presented were corrected to exclude the cases of false multiparasitism i.e., cases in which apparent ovipositional behavior of one of the species did not result in an egg.

It is shown that Aphytis was the winning species in almost all combinations. Only in cases when it attacked hosts containing advanced larvae of Pteroptrix, were the end results less predictable.

The fact that Aphytis is an ectoparasite, piercing the host and sucking its body fluids from the outside, and also has a faster rate of development than Pteroptrix (14 vs. 21 days generation time, respectively, under the conditions of this experiment), provides the former with an advantage over the latter. Thus, when both species oviposit successively in the same host within a short time interval, Pteroptrix will usually be the loser. Even when Aphytis attacks hosts parasitized by young larvae of Pteroptrix, it is able to catch up with its competitor and overcome it (Fig. 4a,b).

Table 2. Intrinsic competition between Aphytis holoxanthus and Pteroptrix smithi in multiparasitized hosts (summary of all replicates).

PARASITE	<u>Aphytis</u> following <u>Pteropt.</u>		<u>Pteropt.</u> following <u>Aphytis</u>	
INSTAR				
IN HOST	Number of successes* to:			
	<u>Aphytis</u>	<u>Pteroptrix</u>	<u>Aphytis</u>	<u>Pteroptrix</u>
Egg	6	2	6	0
L1	6	0	7	0
L2+L3	2	2	0	0

* Corrected values; see text.

Figure 4. Cases of multiparasitism by Aphytis holoxanthus and Pteroptrix smithi:

- (a) Six pupae of Aphytis (Ap) on a host that had contained 1st-instar larvae of Pteroptrix.
- (b) Two pupae of Aphytis and 2 dead 2nd-instar larvae of Pteroptrix (Pt) after the former had parasitized a host containing 1st-instar larvae of the latter.
- (c) A degenerated larva of Aphytis on a mummified host containing healthy larvae of Pteroptrix. When the host was attacked by Aphytis, it had already contained 2nd- or 3rd-instar larvae of Pteroptrix.
- (d) Healthy larva of Aphytis and a deteriorating larva of Pteroptrix. Aphytis attacked the host when it had already contained a 2nd- or 3rd-instar larva of Pteroptrix.
- (e) Multiparasitism in the field: 2 larvae of Aphytis and 2 of Pteroptrix sharing a host; final outcome not clear.

Only on one occasion, when Pteroptrix attacked a host containing eggs of Aphytis, were three healthy larvae of the former and one of the latter found together. Although the final winner could not be determined, it appeared that the development of a single individual of Aphytis brought about relatively slow changes in the host's body, permitting concurrent development of the Pteroptrix larvae. In all other cases where Pteroptrix followed Aphytis, and two or more larvae of the latter were present, Aphytis was dominant. When Aphytis attacked hosts containing young larvae of Pteroptrix, the presence of six Aphytis larvae prevented the development of Pteroptrix (Fig. 4a), whereas two larvae of Aphytis permitted the larvae of Pteroptrix to reach the second instar, at which stage they died (Fig. 4b). Similarly, when Aphytis parasitized hosts containing mature larvae of Pteroptrix, and only one larva of each species inhabited the host, the Pteroptrix larva caused relatively slow changes, enabling the late-coming Aphytis larva to win (Fig. 4d). However, when two Aphytis larvae competed with three Pteroptrix larvae, the latter managed to mummify the host before Aphytis had a chance to develop, and Pteroptrix was the winner (Fig. 4c).

In addition, twenty one cases of multiparasitism were observed in field samples and are presented in Table 3 (see also Fig. 4e). In every case, it was attempted to determine the sequence of attack, based upon the developmental stages found and on their estimated duration of development. Aphytis seemed to be the first in only one case, Pteroptrix in 13, and in 7 events the sequence could not be determined (Table 3). Based on the results of the host discrimination test, the expected outcome of each multiparasitism event in the field was predicted. Aphytis was the expected winner in 12 cases, Pteroptrix in 3, and in the remaining 6 events the winning species could not be predicted. Definite results of multiparasitism were observed in only 4 events (Table 3); in the others, our examination prevented the parasites from completing their development.

It is generally assumed that an ectophagous parasite may be intrinsically superior to an endophagous competitor (Flanders 1971, Vinson & Iwantsch 1980). The evidence presented herein agrees with the

findings of Huffaker & Kennett (1966) about Aphytis paramaculicornis DeBach & Rosen [= "Persian" A. maculicornis (Masi)] and Coccophagoides utilis Doult (Hymenoptera: Aphelinidae), an ecto- and endoparasite, respectively, of the olive scale, Parlatoria oleae (Colvée), in California. Gerson (1968) studied the intrinsic interaction between Aphytis hispanicus (Mercet) and Encarsia (= Prospaltella) inquirenda (Silvestri) (Hymenoptera: Aphelinidae), an ecto- and endoparasite,

Table 3. Multiparasitism in field samples.

CASE NO.	DEVELOPMENTAL STAGES [^]		FIRST SPECIES (ASSUMED)	WINNER (EXPECTED)
	<u>A. holoxanthus</u>	<u>P. smithi</u>		
1.	1E	E	Not clear	<u>A. holoxanthus</u>
2.	2E	2L1	<u>P. smithi</u>	<u>A. holoxanthus</u>
3.	E	1L1	<u>P. smithi</u>	<u>A. holoxanthus</u>
4.	1E	3L2	<u>P. smithi</u>	Not clear
5.	E	3L2	<u>P. smithi</u>	Not clear
6.	E	L	<u>P. smithi</u>	Not clear
7.	1E, 1L2	1L2	<u>P. smithi</u>	<u>A. holoxanthus</u>
8.	4L	4L	Not clear	<u>A. holoxanthus</u>
9.	L	L	Not clear	<u>A. holoxanthus</u>
10.	L	L	Not clear	<u>A. holoxanthus</u>
11.	1L	1L	Not clear	<u>A. holoxanthus</u>
12.	1L	3L	Not clear	Not clear
13.	2L2	4L1	Not clear	<u>A. holoxanthus</u>
14.	2L2	3L2	<u>P. smithi</u>	<u>A. holoxanthus</u>
15.	2L2	2L3	<u>P. smithi</u>	Not clear
16.	1L3	E	<u>A. holoxanthus</u>	<u>A. holoxanthus</u>
17.	3L3	1L3	<u>P. smithi</u>	<u>A. holoxanthus</u>
18.	1L	1P	<u>P. smithi</u>	<u>P. smithi</u>
19.	1L	2P	<u>P. smithi</u>	<u>P. smithi</u>
20.	1L2	3P	<u>P. smithi</u>	<u>P. smithi</u>
21.	1L3	3P	<u>P. smithi</u>	Not clear

[^] E = egg; L = Unclassified larval instar; L1,2,3 = First, second and third instar, respectively; P = pupa.

respectively, of the chaff scale, Parlatoria pergandii Comstock, in Israel. He too found, in laboratory and field observations, that in most cases of multiparasitism A. hispanicus had an advantage over E. inquirenda, as long as the former attacked the host when still soft (i.e., during the first week of development of E. inquirenda). Only when Encarsia brought the host to an advanced stage of mummification

was it able to complete its development and the Aphytis larvae failed to survive. Whenever Encarsia attacked hosts already parasitized by Aphytis, the latter was invariably the winner (Gerson 1968).

In terms of host discrimination ability, representing an interaction between adult wasps, A. holoxanthus appears to hold a slight advantage over P. smithi. In intrinsic competition, Aphytis demonstrated a decisive superiority. The tendency of Aphytis to oviposit in hosts containing eggs of Pteroptrix is compatible with its intrinsic superiority in this situation. On the other hand, the failure of Pteroptrix to avoid hosts containing eggs of Aphytis stands in contrast to its intrinsic inferiority in this situation. Likewise, non-discrimination by Aphytis between hosts containing first-instar larvae of Pteroptrix and healthy ones does not affect its success in interspecific competition, whereas non-discrimination by Pteroptrix in a similar situation does, and is a disadvantage. The fact that both species show ovipositional restraint when faced with hosts containing second and third-instar larvae of their competitors agrees with the outcome of their intrinsic competition under these conditions.

The clear dominance of Aphytis over Pteroptrix in both aspects of competition studied here is in marked contrast with the latter's conspicuous superiority in the field. Similar phenomena were observed in some other host-parasite complexes (DeBach & Sundby 1963, Bartlett & Ball 1964, Gerson 1967, 1968, Wylie 1972b). This can be explained only if both the extrinsic and intrinsic aspects of the interaction are taken into consideration. A parasite species that is intrinsically inferior but extrinsically superior may have an advantage in the field, because intrinsic competition does not directly affect host density, whereas extrinsic competition does (Flanders 1966, 1971, Huffaker *et al.* 1976; see also DeBach & Sundby 1963, Gerson 1967, 1968, Wylie 1972b). Inasmuch as Pteroptrix is intrinsically inferior to Aphytis, and has poorer host discrimination ability, it is possible that its dominance in the field may be explained by examining extrinsic aspects of the interaction, such as the searching ability of the adult wasps, or their susceptibility to weather conditions, to scarcity of food, or to the effect of pesticides.

Mixed populations: Interspecific competition under controlled conditions

So far, this study has dealt with various aspects of interspecific competition between A. holoxanthus and P. smithi on the same host, the Florida red scale, but no direct interaction between the competing species was involved, except for responses to the previous presence of searching adults or short-term competition between larvae upon an individual host. The next step was to study the populations of the two species when allowed to develop together in the same system.

Table 4 summarizes available information about the basic biology of A. holoxanthus and P. smithi. The data in this table indicate that, theoretically, A. holoxanthus has a considerably higher potential for population increase. Whether this species can maintain its advantage in the presence of its competitor was therefore tested in mixed populations.

Table 4. Biological characteristics of Aphytis holoxanthus and of Pteroptrix smithi.

CHARACTERISTIC	<u>Aphytis</u>	<u>Pteroptrix</u> [^]
Sex ratio (F/M)	2:1 ^{^^}	2:1
Eggs/Female	32 ^{^^^}	21
Developmental period at 27°C(days)	13 ^{^^}	22

[^] Data from Bar & Gerling (1971).

^{^^} Data from Rosen & DeBach (1979).

^{^^^} Data from Rao & DeBach (1969).

METHODS

Equal numbers (5-10 pairs) of each species were introduced into plastic cages containing one butternut squash infested with 200-300 Florida red scales, 30-35 days of age. Two additional infested squashes were introduced at 14-day intervals. Each squash was kept in

the system for 30-35 days, and was then transferred to an emergence cage, provided with glass collecting tubes, for 21-25 additional days. Adults emerging in the emergence cages were scored and re-introduced into the mixed-population cage.

The following 3 treatments were applied to different cultures (each in 3 replicates): a. All adult parasites were provided with supplementary food (honey-soaked filter paper) throughout the study period. b. Only those adults which emerged in the emergence cages (but not in the system) and accumulated in the glass tubes were provided with supplementary food (as in treatment a) until their transfer to the system. c. No food was provided to the adults.

In addition to the data obtained from the emergence cages, a sample of 100 scale insects was taken every 14 days in each system, and the rate of parasitism by the two species was determined.

The systems were maintained for several months, or until one of the competing species had disappeared.

RESULTS AND DISCUSSION

When provided with supplementary food (treatment a), A. holoxanthus became the dominant species in ca. 50 days, while P. smithi was completely replaced (Fig. 5a). Following the disappearance of the latter species, the populations of the winner continued to fluctuate over a wide amplitude, which can be related to the effect of the host being a limiting resource.

With partial supply of food to the parasites (treatment b), both species coexisted for longer periods (60-150 days, Fig. 5b). In two replicates, A. holoxanthus eventually displaced P. smithi, whereas in the third one A. holoxanthus disappeared while P. smithi maintained its population, although at a relatively low level.

Without any supplementary food (treatment c), the two species coexisted at fluctuating levels until the experiment was terminated after 190 days.

Figure 5. Changes in populations of *Aphytis holoxanthus* (●) and *Pteroptrix smithi* (o) in mixed cultures. A_{1,2}- with complete adult nutrition; B_{1,2,3}- with partial adult nutrition; C_{1,2,3}- without adult nutrition. Broken line- host was limiting factor.

The introduction of an additional variable (adult nutrition) into the system affected the two parasite species differentially. It cancelled the complete advantage of Aphytis and increased the ability of Pteroptrix to coexist with its competitor. The importance of carbohydrates in the nutrition of a wide range of adult parasitic wasps is now a common knowledge. Gerson (1968) and Avidov et al. (1970) demonstrated its importance in species of Aphytis. Several authors also studied the interactions between endo- and ectoparasitic species attacking the same host. DeBach & Sundby (1963) studied a similar type of parasite complex attacking the California red scale (Aonidiella aurantii), whereas Avidov & Gerson (1968) studied the interactions in the parasite complex attacking the chaff scale (Parlatoria pergandii). However, these studies did not incorporate the effect of adult nutrition, as was done herein.

The results of these experiments reaffirm the advantage of A. holoxanthus over P. smithi under the conditions of this study. As expected, this species proved capable of building high populations at a higher rate than its competitor, and prevented P. smithi from maintaining its own populations. The process involved was interspecific competition, with hosts as a limiting resource. This occurred when adult nutrition was not limited. It should be pointed out that the information on the basic biology of the two species (Table 4) was obtained under similar conditions, where the adults were provided with honey as food. When adult nutrition became a limiting resource, the rate of population increase of A. holoxanthus decreased, thus allowing P. smithi to maintain its populations and coexist for relatively long periods.

Summing up these results, it is evident that under the conditions of the experiment, A. holoxanthus was either the winner or coexisted with P. smithi. However, a reduction of adult nutrition immediately affected the efficiency of A. holoxanthus, reducing its advantage over its competitor, although in most cases this was not sufficient to make P. smithi a consistent winner. Other factors should act differentially in the field for the outcome to be that P. smithi will constantly

become the major species, as seems to occur now in the citrus groves in Israel.

The effect of malathion

The organophosphorus insecticide malathion was introduced into the citrus groves of Israel during the late 1950's, in bait sprays to control the Mediterranean fruit fly (Medfly), Ceratitidis capitata (Wiedemann) (Diptera: Tephritidae). At first it was applied from the ground, but since the late 1960's aerial ultra-low-volume (ULV, 1 liter/hectare) sprays have been used. Although these sprays are applied in 50m-wide strips with 100m in between, Y. Nitzan (Personal communication) showed that fine 200 μ droplets actually drift all over the grove.

Our sampling plots were commercially treated against the Medfly (2-4 aerial treatments per month during September - November, less intensively during August, December, April and May).

Analysis of the rates of parasitism by the two species in the sampling plots revealed some links between the fluctuations in parasitism and the Medfly treatments. The rate of parasitism by Aphytis in the center of the Shefayim plot decreased to 2-6% during the main treatment season (September - December), increased to 16% following the end of the treatments and up to 18% in May, then dropped again to 4% in August when the plot was treated again (about a week before the sample was collected) (Fig. 1). A similar trend was evident on fruit. Parasitism by P. smithi was less affected; it remained high and relatively stable, except in November. A similar differential effect was observed at the margins of the plot. In Gan-Efrayim, total parasitism by these species on leaves oscillated around 50% during winter and reached ca. 90% in August. A similar trend was observed on fruit. Again the major species was P. smithi, while A. holoxanthus, although present, contributed only a small portion to the rate of parasitism (Fig. 2).

METHODS

The bait, Nasiman (Tamogan Ltd.), and the pesticide malathion (produced by American Cyanamid) were tested separately, using the feeding test developed by Havron (1983) for minute parasitic Hymenoptera. After a 3-hour starvation period, adult wasps were confined in adapted Munger cells. Each cell had a depression in its bottom plate, containing the tested solution (either Nasiman, or a sucrose solution with the required concentration of malathion), dyed with red food color (Carmosine, produced by Florum, Tel Aviv) and covered with a disc of filter paper. A coverslip placed on the disc limited the area available for feeding and contact to the circumference. Wasps that fed on the tested solution became visibly dyed, and only they were taken into account in analyzing the results.

In the first test, each of the two species was exposed for 24h to the following treatments: Nasiman, sucrose, Nasiman + sucrose, water. In the second test, the wasps were exposed for 1h to 10% sucrose solutions containing various concentrations of malathion (0, 2.5, 5, 10, 20 and 40ppm for A. holoxanthus, 0, 5, 10, 20, 40 and 60ppm for P. smithi). Survivors were then transferred into ventilated recovery cells containing sucrose, and their survival was recorded after 24h.

RESULTS

Effect of Nasiman: The results are summarized in Table 5. As there was no difference in the effect of the bait on the two species, the data were pooled and are presented as a single value for both species (see Table 5). The mortality on this bait did not differ significantly from that on water.

Addition of sucrose significantly reduced the mortality as compared to the bait alone, but survival on the sucrose-bait combination remained significantly lower than on sucrose alone.

Table 5. Effect of Nasiman on mortality rates of A. holoxanthus and P. smithi.

FOOD	NO. OF INDIVIDUALS EXPOSED		MORTALITY [^]
	<u>A.holoxanthus</u>	<u>P.smithi</u>	<u>A.holox.+P.smithi</u>
Nasiman	244	139	66.47 ^{^^a^^^}
Water	244	164	54.59 a,b
Sucrose+			
Nasiman	257	163	50.39 b
Sucrose	279	150	21.52 c

[^] Data of both species were pooled, as there was no significant difference between the two.

^{^^} Values after angular transformation.

^{^^^} Different letters indicate significant differences at $\alpha = 0.05$.

Effect of malathion: The results are presented in Fig. 6. Under the conditions of this test, A. holoxanthus was found to be considerably more sensitive to malathion than P. smithi (Log LC₅₀=0.67 and 1.28, respectively).

Figure 6. Concentration-response curves of (●) Aphytis holoxanthus and of (○) Pteroptrix smithi to malathion.

DISCUSSION

The results of our laboratory tests are in agreement with field evidence as to the differential effect of malathion - the active ingredient in the Medfly bait sprays - on the two parasites. It is possible that this differential effect is one of the main factors responsible for the current composition of the parasite complex of the Florida red scale. This appears to be corroborated by the following comparative notes from the history of pest control on citrus in Israel:

1959/60 - Summer bait-spray treatments instituted in addition to the winter sprays. First evidence of establishment and initial dispersal of P. smithi.

1967 - U.L.V. aerial bait sprays. P. smithi increases, A. holoxanthus decreases.

Further indirect evidence indicates that this hypothesis, on the selective detrimental effect of malathion on A. holoxanthus, may perhaps be applicable also to other broad-spectrum insecticides. Thus, on Sept. 9, 1981, the sampling plot in Shefayim was treated with a mixture of carbaryl (a carbamate) and formothion (an organophosphate). Prior to this treatment, both parasite species were present in this plot, but for three months thereafter only P. smithi was recorded in leaf samples. In June 1981, the citrus grove of Nir Eliyahu was treated with methidathion (an organophosphate). The grove was sampled three months later and all Florida red scales on the leaves were found dead, so that they could be taken to represent the state of parasitism prior to the treatment. Out of ca. 1000 scale insects sampled, 45% showed emergence holes typical of A. holoxanthus, whereas only ca. 6% showed evidence of P. smithi. On fruits, on the other hand, there were live scale insects, and out of 138 only 1.5% were parasitized by A. holoxanthus, as compared to 86% parasitized by P. smithi. If the fruit sample is indicative of the post-treatment situation, it again appears that A. holoxanthus was more affected than P. smithi by this treatment.

A. holoxanthus vs. P. smithi: r vs. K strategists?

The terms r- and K-selection were first suggested by MacArthur & Wilson (1967) in relation to their "island theory" on the processes of colonization and survival in isolated ecosystems. "r" denotes the intrinsic rate of natural increase of an organism, whereas "K" describes the carrying capacity of the ecosystem.

r-strategist organisms are the first to colonize an ecological "vacuum" following natural or man-made catastrophies. Their populations increase rapidly without the pressure of intra- or interspecific competition. Such organisms allocate maximum energy to produce a maximal number of progeny per time unit. A typical r-strategist is small, energy inefficient, has a short generation time, a low competitive ability and a high reproductive rate. A typical K-strategist, on the other hand, is big, efficient in using the energy resources in the environment, has a low rate of reproduction and a high interspecific competitive ability. Southwood et al. (1974) added another parameter to define r- vs. K-strategists: the ratio between generation time (τ), and the time period during which the overall conditions in the ecosystem are favorable for the organism (H). For an r-strategist, $\tau/H=1$, whereas for a K-strategist $\tau/H<1$.

These terms are relative. One may visualize a continuum, with r and K at the two extremes (Pianka 1970). The species occurring in each ecosystem may be placed at different points along this range, according to their various attributes. Generally, insects and other invertebrates are located toward the r- end, whereas vertebrates are located toward the K-end (Pianka 1970). However, such discrimination can be carried out also within each group of organisms. Within the insects, for example, the Lepidoptera are considered r-strategists in relation to the Coleoptera (Stubbs 1977), and within the Lepidoptera, certain species are more r-oriented, whereas others are more K-oriented (Southwood 1974). Microorganisms may also be characterized in these terms (Gerson & Chet 1981).

Introduction of a natural enemy into a new habitat is similar to the colonization of islands as described by McArthur & Wilson (1967). During the first phase, when the pest population is high, the r-strategists among the introduced natural enemies are expected to increase, whereas in later phases, those that tend towards K-strategy are expected to take over gradually and eventually replace the former. Several authors have attempted to place various species of natural enemies, attacking the same host, along the r-K continuum in accordance with their attributes (e.g., Force 1970, 1972, 1974, 1975, Price 1970b). Of course, the main problem in this respect is how to define the particular attributes of a natural enemy that contribute towards an r- or K- strategy.

Force (1974) made the practical suggestion that only r-strategist natural enemies be sought in the pest's area of origin and imported into the new habitat. Unfortunately, his suggestion ignores the later stages of the natural enemy - pest interaction. A more reasonable approach would be to introduce r-strategist natural enemies into unstable ecosystems, such as seasonal field crops (Ehler & van den Bosch 1974) and K-strategists into more stable ecosystems such as orchards and other perennial crops (Ehler 1982a).

Evaluation of the various attributes of A. holoxanthus and P. smithi in view of their relative contribution to the two strategies (Table 6) indicates that, overall, the former is more r-oriented whereas the latter is more K-oriented.

When one attempts to determine the relative position of each attribute along the r-K continuum (Fig. 7), this impression is enhanced: A. holoxanthus appears to be relatively more of an r-strategist, whereas P. smithi is more of a K-strategist.

Figure 7. Comparison of several attributes of (●) Aphytis holoxanthus and (o) Pteroptrix smithi on the r--K continuum. 1. r_m , 2. Searching capacity, 3. Host specificity, 4. Tolerance to malathion, 5. Host discrimination and in-host competitive ability, 6. Host utilization, 7. Body size.

Table 6. Comparison of A. holoxanthus to P. smithi in view of r- and K- strategies.

ATTRIBUTE	<u>A. holoxanthus</u>	r-vs.K-	<u>P. smithi</u>	r-vs.K-
r_m	0.35 (Sharoni 1980)	r	0.17 (Bar 1969)	K
<u>Specificity</u>				
host range	3 host species	r	single host	K
Stages (in Florida red scale)	L2, Female, Male pupa	r	L2, Female	K
<u>Body size</u>	Male 0.82 (Rosen&DeBach 1978)		Male 0.55 (Bar 1969)	
(mm)	Female 1.05	r	Female 0.75	r
<u>Host-utilization</u>				
Oviposition(min)	10 - 15	r	35 - 40	K
Progeny/host ^{^^}	2.4	r	3.9	K
Host feeding	Yes (Rosen 1964)	r	No (Bar 1969)	K
Sensitivity to malathion (LC ₅₀)	4.84	r	19.91	K
<u>Out- and In- host comparison</u>				
Searching ability	Inferior	r	Superior	K
Discrimination ability	Superior	K	Inferior	r
Intra-host competition	Winner	K	Loser	r
G/H ^{^^^}	=1	r	<1	K

[^] Calculated from table of daily oviposition and from sex ratio, female fecundity and rate of development.

^{^^} Females of Florida red scale.

^{^^^} G = generation time; H = period of time that the environment is favorable for the organism.

Indeed, analysis of the processes that have taken place since the simultaneous introduction of these species into Israel does not

contradict these assumptions. As already mentioned, the population of A. holoxanthus increased rapidly following its introduction, as befits an r-strategist, and reduced the populations of the Florida red scale below the economic threshold. P. smithi, on the other hand, was initially established very slowly and did not contribute much, if anything, to the spectacular biological control of the pest. Later, however, its populations began to increase and spread, gradually replacing those of A. holoxanthus, until it has become the major natural enemy in residual host populations. Such performance is, of course, typical of a K-strategist.

2. The endoparasite *Comperiella bifasciata* Howard, and its interactions with ectoparasites of the genus *Aphytis* in the California red scale

The California red scale, *Aonidiella aurantii* (Maskell) (Homoptera: Diaspididae), is a major pest of citrus in Israel and elsewhere. Species of the aphelinid genus *Aphytis* have played a major role in the biological control of this pest (Rosen & DeBach 1978, 1979). In California, *A. chrysomphali* (Mercet) was the only species of this genus attacking the California red scale until 1948, when the introduction of *A. lingnanensis* Compere brought about a marked decrease in its importance. Several years later, when *A. melinus* DeBach was also introduced and established in California, an entirely new situation developed, which is discussed in Section 2 of this report.

In Israel, too, *A. chrysomphali* was the only species of *Aphytis* parasitic upon the California red scale until the late 1950's. In 1960, *A. coheni* DeBach was discovered attacking this pest in Israel. Although it is possible that this species accidentally reached Israel on its own accord, it might also have been unintentionally introduced from Hong Kong together with *A. holoxanthus* (Rivnay 1968, Rosen & DeBach 1978, 1979). Several other species have been introduced into Israel since then, including *A. melinus* in 1961. Currently, the California red scale in Israel is attacked by *A. chrysomphali*, *A. coheni* and *A. melinus*, and several studies have been published on the relative abundance of these species (e.g., Avidov *et al.* 1970, Kamburov 1973).

Comperiella bifasciata Howard (Hymenoptera: Encyrtidae), a solitary endoparasite, has also been introduced into Israel against the California red scale. Early introductions in 1936, 1945 and 1950 failed (Rivnay 1968), and establishment of this species was achieved only following mass releases made during 1961-1964. By 1968, *C. bifasciata* was recorded in the southern coastal plain of Israel (Kamburov 1973) as well as in other parts of the country (Rosen 1974, Baum 1979).

This species is generally considered as inefficient (e.g., DeBach & Sundby 1963, DeBach et al. 1971). In Israel, however, although its contribution to the regulation of the pest's population was not studied intensively, Baum (1979) reported parasitism of up to 80% on fruit and 30% on leaves.

The interactions between Comperiella and Aphytis were studied under controlled conditions as well as in the field.

General biology of C. bifasciata

The literature on C. bifasciata lacks information about important biological aspects, and whatever data are available are often contradictory and inapplicable to the conditions of Israel. For a meaningful study of the interactions of this species with Aphytis, a preliminary biological study was therefore required. This included the following aspects: 1. Ovipositional behavior (presented in Fig. 8).

Figure 8. Behavioral sequence leading to oviposition in Comperiella bifasciata.

2. Daily oviposition and survival (Figs. 9a,b); a comparison of the data obtained on these aspects in the present study with information published by other authors is presented in Table 7.

Figure 9. *Comperiella bifasciata*: (a) Survival and (b) Cumulative daily oviposition when provided with different foods (o= honey, ●= honey+water, ■ = total oviposition).

Table 7. Comparison of biological data published on *Comperiella bifasciata* to the results of the current study.

	GF(1)	OR(2)	LE(2)	LE(3)	LE(4)	FRUIT(5)	L.DIS(6)
Progeny (mean)	23.5	11.5	4.4	30.6	47.8	50	10
Range	15-31			21-47	5-95	?-136	4-18
Females (%)	52.1			75.2	54.9	50	
Longevity (days)	5.3	>14	<14	37	6-7	10	24.6

GF= grapefruits; OR= oranges; LE= lemons; L.DIS= leaf discs.

1= Results obtained in the current study. 2= Results published by Simmonds (1944). 3= Results published by Teran & DeBach (1963). 4= Results published by DeBach & Sundby (1963). 5= Results published by Flanders (1944). 6= Results published by Brewer (1971).

3. Host stage preference . A clear preference of the young females (YF) over the mature female (MF) and over the second moult by the parasite can be clearly seen in the results presented in Table 8.

Table 8. Host stage preference of Comperiella bifasciata (attacking California red scale on grapefruits).

REPLICATE	DEVELOPMENTAL STAGE OF HOST^		G-test	Probability
	YF	MF		
1	65	30	13.2	<0.001
2	51	7	37.7	<0.001
3	55	14	25.0	<0.001
			G-pooled=68.9	<0.001
1	YF	M2	3.4	>0.05
	46	30		
1	F-YF	MF	0.37	>0.60
	36	31		

^ YF, MF, M2= Young female, mature female and second moult, respectively.

4. Effect of temperature on the rate of development. This was studied at 12 constant temperatures, ranging between 16 and 36°C, and on two different host plants, squash and grapefruit (Fig. 10). The highest rate of development was achieved at 32°C, and the calculated lower threshold of development was 14.9°C. The best equation to describe the effect of temperature on the rate of development (up to 32°C) of the parasite was found to be a polynom of the second order:

$$\text{RATE} = -0.00626x(\text{TEMP} - 45.85)^2 + 6.014$$

Figure 10. Developmental rate of Comperiella bifasciata in hosts infesting different fruits at constant temperatures.

(□)(■)(▣)- Squash; (○)(●)(◐)- Grapefruit; (▲)- Mean of all replicates.

Interspecific discrimination of parasitized hosts

As pointed out in the first chapter of this report (p. 8), several species of parasitic Hymenoptera are known to be capable of detecting hosts already parasitized by other species (e.g., Weseloh 1983). Such discriminative ability can increase the efficiency of a parasite by reducing progeny wastage and by distributing attacks on a higher proportion of suitable hosts, thus causing a higher rate of parasitism.

The ability of C. bifasciata to detect hosts parasitized by Aphytis and vice versa, was investigated in the study reported herein.

METHODS

Oviposition cells (glass cylinders, 2.5cm in diameter and 2cm high) were attached with plastic glue to grapefruits infested with the California red scale. A female wasp (*C. bifasciata* or *A. melinus*), up to 48h in age, was separated from hosts for 24h and then introduced into the cage. Her behavior was observed and recorded for several hours, and the hosts parasitized by her were marked. The wasp was then replaced by a female of the other species, and the behavior of the second female was recorded for 2h. The second female was then removed and the fruits were placed at 27°C for 12-13 days, after which all the scale insects were dissected and checked for parasitism.

The results were analyzed as follows: First the expected rate of multiple parasitism was calculated, assuming random distribution of encounters; then, the difference between the observed and calculated values was analyzed, using both a t-test for paired observations (as used by Weseloh 1983) and linear regression (Griffith 1969).

RESULTS AND DISCUSSION

Both species did not exhibit a clear response to hosts already parasitized by the other species: No indication of either avoidance or attraction was observed (Tables 9, 10 and Fig. 11).

Table 9. Oviposition by *Aphytis melinus* following previous parasitism by *Comperiella bifasciata*.

REPLICATE NO.	NO. OF HOSTS:		OVIPOSITION	EXPEC.NO.	OBSER.
	TOTAL	PAR.BY SP.I	<i>A. melinus</i>	OV. IN	OV. IN
	H	I	II	HOST II*I/H	PARAS. HOST
1.	20	6	4	1.2	1
2.	33	11	3	1.0	3
3.	30	4	5	0.667	0
4.	36	7	6	1.167	1
5.	17	5	4	1.176	5
6.	36	9	6	1.333	5

t = Test for paired observations, t = 1.06; p = 0.34 Not significant.

Comperiella distributed its eggs in an entirely random manner (t-test for paired observations not significant, regression line between observed and expected significant with correlation coefficient $R=0.7955$, slope not different from 1.0 and intercept not different from 0). The response of Aphytis was less predictable. In some cases the female demonstrated a clear avoidance, in others no response, and in still others even attraction to already parasitized hosts. Of the 24 cases of multiple parasitism, Aphytis was the winner in 12, Comperiella in 3, and both the host and the parasites died in 9 cases. The fact that both parasites do not avoid hosts already parasitized by the other species can affect their efficiency. The effect of such behavior on C. bifasciata should be more pronounced, as this species appears to have a lower probability of completing its development in cases of multiple parasitism. Aphytis also holds the advantage of a higher developmental rate. Even so, a high degree of progeny wastage occurred in the cases of multiple parasitism (88% in C. bifasciata, 50% in Aphytis) which, of course, would be reduced had the mechanism of host marking and interspecific discrimination been more developed in both species.

Table 10. Oviposition of Comperiella bifasciata following previous parasitism by Aphytis melinus.

REPLICATE NO.	NO. OF HOSTS:		OVIPOSITION	EXPEC.NO.	OBSER.
	TOTAL	PAR.BY SP.I	<u>C.bifasciata</u>	OV. IN HOST II*I/H	OV. IN PARAS HOST
	H	I	II		
1.	8	2	3	0.75	1
2.	23	2	3	0.26	1
3.	16	5	8	2.5	4
4.	36	4	12	1.33	3
5.	24	7	11	3.21	4
6.	16	4	3	0.75	0
7.	21	5	1	1.91	1
8.	21	1	1	0.05	1

t - Test for paired observations, $t = 1.58$; $p = 0.22$ Not significant.

Figure 11. Oviposition of (Δ) *Aphytis melinus* and (o) *Comperiella bifasciata* following prior attack by the other species. Ratio between expected to observed parasitism, assuming no detection of already parasitized hosts. Rejection= Area of avoidance of superparasitism, Attraction= Area of attraction of the parasite to already parasitized hosts. (---) Observed (---) Expected. Equation of line:

$$\text{Observed} = 0.38 + 1.11 \times \text{Expected}; r = 0.7955$$

Mixed populations: Interspecific competition

In the previous experiments, each species was studied separately. The next step was to study interspecific competition between these species in closed systems (cages), where adults competed for suitable hosts while the larvae competed for successful development.

The reader should bear in mind that the California red scale is suitable for parasitism by *Aphytis* for a very short period. While parasitism can occur during L2, YF and male pupa, only YF, which is at age of 21-25 days at 27°C (see also Luck & Podoler, 1984) is suitable for female progeny production. Although *Comperiella* also prefers this stage, it is capable of parasitizing and developing in younger as well as older hosts. Competition between these species may therefore be considered, at least in part, a time-successive competition (Flanders 1971).

With a limited host supply, the mechanisms of avoiding both superparasitism and multiple parasitism may collapse. In such cases, especially in those of multiple parasitism, Aphytis has a clear advantage over its competitor. Similar studies were carried out by DeBach & Sundby (1963) for C. bifasciata and A. lingnanensis.

Table 11 presents several parameters which describe the theoretical rate of increase of single-species populations of these parasites. The shorter developmental period of A. melinus, coupled with its longer adult female survival and facultative gregariousness, provide this species with an advantage over Comperiella as far as their expected rate of increase and ability to utilize hosts are concerned.

Table 11. Population parameters of Aphytis melinus and of Comperiella bifasciata.

	<u>Aphytis melinus</u>	<u>Comperiaella bifasciata</u>
Oviposition	24 eggs/female	25 progeny/female
Generation	13-14 days	31 (28-33) days
Gregarious.	In large scale insects	Obligatory solitariness
Females (%)	75	65 (field & laboratoty)
Host feeding	Common	Rare or absent
Longevity (females)	10 days	6 - 7 days
Females after 60d [^]	ca. 5800(4 generations)	ca. 1440 (2 generations)

[^]- Calculated assuming exponential growth with initial population of 10.

The following system was designed to study the interactions of the two species in mixed populations.

METHODS

The system was initiated by introducing 10 pairs of newly-emerged wasps (up to 24h in age) of each of the two species into a cage containing one grapefruit infested with 21-23-days-old California red scale. One additional infested grapefruit was introduced every week for the next 5 weeks, and thereafter the new fruit was used to replace the oldest one, which was removed from the cage. Thus, each fruit was

exposed in the cage for 6 weeks, during which period the host produced a new generation, Aphytis could produce two full generations, and Comperiella about 1.5 generations. The fruits removed from the system were kept for four weeks in separate cages, and the wasps emerging in them were scored and returned to the original system.

The following data were collected weekly: a) Number of adult parasites in the system. This was done either by attracting the wasps to light, or, when the total population exceeded 100, by using CO₂ to anesthetize them. b) Sampling the hosts for rate of parasitism. Samples of 50 hosts were taken from grapefruits which had stayed 14 days in the system. The hosts were dissected with entomological pins under a stereoscopic microscope. Superparasitism was determined when more than a single larva of Comperiella, or larvae of different instars of Aphytis, were discovered in a single host (Luck et al. 1982).

The experiment was conducted in 5 replicates.

RESULTS AND DISCUSSION

The results are presented as time-related population changes (Fig. 12) and, assuming that interactions between the two parasite species do occur, as the adult population of Aphytis vs. C. bifasciata relationships (Fig. 13). To acquire better understanding of the system, the data published by DeBach & Sundby (1963) for A. lingnanensis vs. C. bifasciata were reanalyzed and are presented in a similar way (Fig. 14). The population curves of both species show frequent peaks (=short cycles) e.g., after 30, 52, 84 and 154 days for C. bifasciata, and after 17, 38, 70 and 154 days for Aphytis (Fig. 12). These peaks roughly correspond to the generation time of these species. In addition to these "short cycle" peaks, "long cycles" (of 80-90 days) can also be observed. There are two such cycles in replicate 1 (Fig. 12), whereas the other replicates were terminated before completing one long cycle. In the figure based on DeBach & Sundby's data (Fig 14), the "short cycles" are not evident, probably because of their sampling frequency, however, two long" cycles each

with a frequency of about 100 days, are clearly evident, although their amplitude varied considerably.

Figure 12. Changes in the population (I) and in the rate of parasitism (II) of *Comperiella bifasciata* (o) and of *Aphytis melinus* (Δ) in mixed population cultures. The numbers represent the different replicates; *= multiple parasitism in the sample.

The results of our 5 replicates were not uniform. Aphytis won in two replicates (1, 5) and the population of Comperiella in them decreased to very low levels. In the other three replicates, Comperiella was the winner and Aphytis failed to establish a population. In the absence of its competitor, the population of Comperiella reached an average level of 200, whereas in the presence of Aphytis it decreased to only a few individuals. When Aphytis managed to establish a population in the first few generations, it became the winner, although it could not replace Comperiella completely. These results may be related to the strict dependence of Aphytis on a specific host age: When it did not succeed in establishing an initial population during the first few days following its introduction, it was outcompeted by the less age-specific Comperiella. In DeBach & Sundby's system, there was a marked increase in the population peaks of Aphytis, while those of Comperiella decreased, similar to replicates 1, 5 in the present study. Their data also permitted comparison of populations with and without interspecific competition, and it appears that such competition lowered the amplitude of the fluctuations in both species, especially in Comperiella.

Of special interest is the frequency of the long cycles, which appear to be independent of generation time in both species: ca. 100 days for both species in DeBach & Sundby's study, about 85 days in the present investigation. A similar phenomenon was reported by Avidov & Gerson (1968) for Aphytis hispanicus (Mercet) and Encarsia inquirenda (Silvestri) on the chaff scale, Parlatoria pergandii Comstock.

The overlapping of the long cycles for both competing species, observed under conditions of constant host supply, was evident also in single-species populations (DeBach & Sundby 1963). Such population fluctuations may be indicative of exploitative competition (Price 1975).

Figure 13. Population changes of *Aphytis melinus* in the presence of *Comperiella bifasciata*. Numbers represent the different replicates. e-- mark the end of the experiment.

Figure 14. a. Changes in the populations of *Comperiella bifasciata* (●)(○) and of *Aphytis lingnanensis* (■)(□) in separate (full signs) and mixed (hollow signs) cultures (data from DeBach & Sundby 1963). b. As above, but data presented as one species vs. the other.

Interspecific competition between Comperiella and Aphytis in the
citrus grove

The interaction between the two species in the field was studied in an 80-acre grapefruit grove of Kibbutz Gal'On, in the northern Negev, Israel.

METHODS

The following methods were employed: (A) fruit sampling; (B) exposure of infested fruit in the grove.

(A) Four successive samples, each comprising 21 grapefruits, were collected during winter 1983. Only fruits carrying at least four young females of the California red scale were included in the samples. All young female hosts were numbered, and the fruits were placed singly in plastic boxes for two weeks. The emergent adult parasites were then scored, and the marked hosts were dissected and checked for parasitism.

(B) During June 1983 (after fruit picking), 40 infested grapefruits, each carrying 200 scale insects (21-day-old-females) were placed in the citrus grove. The fruits were hung in plastic nets in the southern quadrant of the trees, shaded from direct sunlight, at a height of 1.5m. One fruit was placed in every second tree in 4 adjacent rows. The fruits were brought back to the laboratory after 8 days, and were placed singly in plastic jars for parasite emergence.

DATA ANALYSIS

In both methods, the fruits were first divided into 4 groups: 1, 2 - hosts parasitized by one species or the other; 3 - hosts parasitized by both species; 4 - unparasitized hosts.

The number of fruits in each group was tested for independence in a 2x2 contingency table, using the χ^2 test (Sokal & Rohlf 1981).

Dependence between groups (=significant χ^2) would indicate that parasitism by the two species is distributed in a non-random manner.

The next step was to test and analyze the response of each parasite species to its competitor. This was carried out, as suggested by Ehler (1979a), by comparing the rate of parasitism of each species when alone on the fruits to that when it was present together with its competitor. A comparison was also made of the total rate of parasitism by both species when on the same fruit, and when one or the other was present alone. The means were compared, using the t-test, and the variance of the means was also calculated. Angular transformation was applied to the proportions before the analysis was made.

RESULTS

Two species of parasites, Comperiella and A. chrysomphali, emerged in both treatments. A. melinus was not present.

Method A. No significant difference was found between the 4 successive samples taken during winter. All these results were therefore pooled. A. chrysomphali was the dominant parasite during this season, and was recorded as the only species on 44% of the fruits. Comperiella was recorded alone on 4%, and both species were recorded together on 5% of the fruits. No response of one species to the presence of the other was detected, which may have been related to the low rate of parasitism by Comperiella. As can be seen in Fig. 15, the total rate of parasitism on fruits where both parasite species were present was significantly higher than when only one species was present. However, the rates of parasitism by each species on these fruits did not differ from those on fruits where only a single parasite species was found. Therefore, it can be assumed that competition did not take place in the system under study.

The results were different on infested fruits exposed in summer. The activity of Comperiella increased markedly. A. melinus was again absent, but A. chrysomphali maintained its population. The test for independence showed that the distribution of parasitized scale insects differed from random (Table 12).

Table 12. Test for randomness in discovering the fruits by both parasite species. (χ^2 test for independence, 2x2 contingency table).

	<u>A. chrysomphali</u>		
<u>C. bifasciata</u>	3.33 [^] (3) ^{^^}	3.67 (4)	7
	36.67 (37)	40.33 (40)	77
TOTAL	40	44	84

[^] Expected values.

^{^^} Values in parenthesis represent the observed data.

Figure 15. Mean percentage of parasitism by *Aphytis chrysomphali* (▨) and *Comperiella bifasciata* (▤) and total parasitism (▧). Numbers indicate significance level (t-test).

There were significantly more fruits without any parasitism than expected. There was also a significant increase in the number of parasites emerging from hosts on fruits parasitized with both species than from single-species parasitism (Fig. 16).

Figure 16. Mean number of progeny of *Aphytis chrysomphali* (▨), and of *Comperiella bifasciata* (▤) and the total (▩) that emerged from fruits inhabited by both species. P = the significance level of differences between means (t-test).

The main contribution to this effect was from the increase in parasitism by *Comperiella*. A correlation was also observed between the number of parasites of each species and that of its competitor on the same fruit (Fig. 17). Table 13 presents the results obtained by the two methods, in the two seasons, in summary form.

Figure 17. Number of progeny of *Comperiella bifasciata* vs. that of *Aphytis chrysomphali* on fruits inhabited by both species (Method B). The equation of the line: $Y = 0.897x + 9.375$, $r = 0.852$, $p < 0.01$.

Table 13. Mean number of progeny per fruit in both methods.

GROUP	METHOD A [^]	METHOD B ^{^^}
<u>Aphytis</u> alone	4.59 (h)	4.33 (a)
<u>Comperiella</u> alone	2.33 (h)	3.75 (a)
<u>Aphytis</u> common ^{^^^}	4.00 (h)	5.78 (a)
<u>Comperiella</u> common	3.25 (h)	14.56 (b)
Both species	7.25 (i)	20.33 (c)

[^] Grapefruits collected in the field.

^{^^} Infested grapefruits exposed in the field.

^{^^^} Inhabited by both parasite species.

The distribution of the two parasites in the citrus grove

This was analyzed from the data obtained when infested fruits were exposed in the citrus grove. Fig. 18 provides the distribution of the fruits and the two parasites.

Table 14a,b summarizes the analysis of these distributions. The parameters used were: 1) Ratio of variance to mean (s^2/x) (Myers 1978, Southwood 1978); 2) Index of dispersion (I_D), calculated as follows:

$$I_D = (s^2/x)(n-1)$$

Where n=number of samples. The distribution of this index is similar to that of χ^2 (Southwood 1978); 3) Index of mean crowding (m^*) (Lloyd 1967), as suggested by Iwao (1968): $m^* = x + (s^2/x - 1)$.

Figure 18. Schematic map describing the distribution of the progeny of the parasites emerging from the grapefruits exposed in the citrus grove (Method B, see text). Each circle represents a single fruit; the numbers within the circles describe the number of emerging parasites: Comperiella bifasciata (upper left half) and Aphytis chrysomphali (lower right half).

The distribution of both parasite species, when alone and when present together, was found to be clumped, with Comperiella demonstrating a higher rate of gregariousness than Aphytis. Moreover, both species increased their aggregation on those fruits with combined parastism, which might indicate that each responded positively to the presence of the other species.

Table 14. Comparison of coefficients to describe: (a) Distribution of the progeny of Aphytis and of Comperiella on grapefruits.

	SPECIES	$s^2/x^{\wedge}$	$I_D^{\wedge\wedge}$	$m^{*^{\wedge\wedge\wedge}}$
METHOD A	<u>Aphytis</u>	3.180	149.5	4.722
	<u>Comperiella</u>	3.251	152.8	2.667
METHOD B	<u>Aphytis</u>	7.938	309.6	9.540
	<u>Comperiella</u>	14.190	567.7	15.840

(b) Distribution of the different groups between grapefruits.

	COMBINATION	$s^2/x^{\wedge}$	$I_D^{\wedge\wedge}$	$m^{*^{\wedge\wedge\wedge}}$
MEHTOD A	<u>Aphytis</u> alone	3.341	147.0	4.697
	<u>Aphytis</u> , common##	4.187	25.16#	5.473
	<u>Comper.</u> common ##	2.907	125.0	2.066
	<u>Comperiella</u> alone	3.717	163.5	3.066
METHOD B	<u>Aphytis</u> alone	6.093	182.75	6.770
	<u>Aphytis</u> , common##	11.450	309.20	12.310
	<u>Comper.</u> , common##	15.23	533.10	17.870
	<u>Comperiella</u> alone	8.380	251.50	7.867

$\wedge$ Coefficient of dispersion.

$\wedge\wedge$ Index of dispersion.

$\wedge\wedge\wedge$ Mean crowding.

Low value resulting from low number of samples.

Fruits inhabited by both parasite species.

Response of *A. chrysomphali* to host density

INTRODUCTION

The quantitative effect of parasites on different densities of their hosts is important to the ability of these biological control agents to regulate the populations of their hosts (e.g., van Lenteren & Bakker 1978).

Solomon (1949) distinguished between functional and numerical responses of natural enemies to host density, where the first pertains to changes in the numbers of hosts attacked by the parasite as a function of host density, and the second to changes in parasite population density as a function of host density.

Holling (1959a,b) recognized 3 categories of functional response: The first, where the number of hosts attacked is directly related to host density (up to a saturation point); the second where the number of hosts attacked by the parasite increases at a decreasing rate as a result of the time allotted to check and to consume the host and to rest (= handling time); and the third, where the number of hosts attacked increases at changing rates (a sigmoid function). Only a parasite exhibiting a sigmoid response curve to host density is able to regulate the population of its host when acting alone (Holling 1959a).

In the following section we shall try to analyze the data obtained in the present study, in order to find whether the type of response of the two parasite species to host density can be detected.

METHODS

The observations on the rate of parasitism on grapefruits in a commercial citrus grove provided the data for this analysis.

RESULTS

The distribution and density of the California red scale (YF) on the grapefruits are presented in Fig. 19. As is shown in this figure, the frequency of host densities on fruits discovered and attacked by *Aphytis* did not differ from that on fruits which were not discovered. This was also substantiated by the insignificance of the χ^2 test for differences between distributions. It can be concluded that, in the system under study, *Aphytis* did not aggregate on fruits containing higher host densities. However, there was a significant linear relationship between the density of suitable hosts (YF) on a given grapefruit and the number of *Aphytis* adults emerging from them ($Y = -2.71 + 0.615X$, $P > 0.001$, $R^2 = 0.821$). This relationship can be considered a "Type 1" functional response.

Figure 19. Frequency of fruits carrying different densities of suitable hosts (young females of California red scale). Frequency of fruits: all infested fruits (□); discovered by *Aphytis* (▨); discovered by *Comperiella*; (▧) discovered by both species (▩).

The slope of the line can serve as one of the parameters in evaluating parasite efficiency (DeBach et al. 1976).

Varley & Gradwell (1968) suggested that a linear relationship between the population surviving parasitism (S) and the population exposed to the mortality factor (N) (both following logarithmic

transformation) indicates the presence of a density dependent mortality factor. Benson (1973) added that in order to determine such a relationship, the ratio $\log N / \log S$ should be examined with the null hypothesis being $b=1$, $a=0$ (acceptance of the null hypothesis meaning that mortality is not density dependent). This relationship is presented in Fig. 20. The line obtained is described by the equation:

$$\log S = -0.227 + 1.036 \log N$$

$R^2 = 0.908$, b does not differ significantly from 1.0, and a differs significantly from 0. Such a relationship, where the line is not going through the origin but the intercept differs significantly from 0, indicates that the mortality factor is responsible for a constant rate of mortality at the whole range of host densities studied (Benson 1973).

Figure 20. The ratio between the number of hosts not attacked by *Aphytis* ($\log S$), and the total number of available hosts on grapefruits ($\log N$).

-2- Calculated according to observed data, $\log S = -0.227 + 1.036 \log N$
 $R^2 = 0.908$; - - - $\log S = \log N$.

DISCUSSION

Both methods used in the present study have demonstrated that parasite efficiency increases when both species are operating together

in the system. Both total rate of parasitism (Method A) and the number of parasites produced per each fruit (both methods) increased. Ehler (1978, 1979a & b, 1982a) also reported an increase in the overall rate of parasitism when more than a single species was present in the system. Moreover, he concluded that this is a general phenomenon of interspecific competition which, although reducing the efficiency of the individual parasite species, increases their cumulative effect (Ehler 1979a).

COMPARISON BETWEEN THE PARASITE SPECIES - SUMMARY

An efficient biological agent can regulate the population of its host and maintain it below the economic threshold. Such a parasite will be able to respond to changes in host density and parasitize increasing proportions of the host population as host density increases (Rosen & Huffaker 1983).

Rosen & Huffaker (1983) discuss four main attributes of an efficient natural enemy: searching capacity, host specificity, ability for population increase and fitness and adaptability.

Searching capacity - This parameter was discussed, described and quantified by numerous authors (e.g. Rosen & Huffaker 1983, Huffaker et al. 1977). However, although this is a major attribute determining parasite efficiency, (e.g., Flanders 1966, Huffaker et al. 1977) there are no straightforward methods to estimate it in the field, and only indirect methods have to be employed.

During the first period of establishment in a new environment, mobility and dispersal ability are important characteristics. Comperiella was inferior to Aphytis in these attributes both in California (DeBach & Sundby 1963) and in Israel (Kamburov 1973). An efficient natural enemy is expected to respond to both its own and its host's density (Rosen & Huffaker 1983). Indeed, Aphytis was detected in more samples than Comperiella, and the former's distribution corresponded to that of the host on the fruits. It may be concluded that this species searched and discovered a higher proportion of the

area where hosts were available. This may be considered as high searching ability (Flanders 1947). Comperiella demonstrated a more clumped distribution.

Other attributes related to searching capacity is the survivorship of the searching females, in which again Aphytis is superior to Comperiella (6-7 vs. 10 days, respectively) and the ability to detect kairomones. This was indicated for Aphytis by Sternlicht (1973) but has not been studied in Comperiella.

Host specificity - This attribute is considered important for an efficient natural enemy and, indeed, most successful biological control operations were achieved by using host-specific parasites. Among the parasites in the present study, Comperiella is the most host specific, attacking only the California red scale. Carroll (1979) argues that the association between this parasite and its host is relatively new (based on the high rate of encapsulation and the concentration of the parasite on fruits, as compared to leaves and branches). However, the fact that the host can continue to produce progeny even when parasitized by Comperiella, together with lower rates of encapsulation observed in Israel (Auerbach 1984), might indicate a prolonged association and co-adaptation between this parasite and the California red scale. Unlike Comperiella, the Aphytis species studied herein can both develop in additional hosts.

Reproductivity - A high reproductive rate, as compared to that of the host, is important, especially in variable environments (e.g., Rosen & Huffaker 1983). The reproductive rate of Aphytis is higher than that of Comperiella.

Fitness and adaptability - By fitness we mean the ability of the natural enemy to survive and reproduce in variable environments. Biological and physiological synchronization with the host are essential attributes within the overall term of fitness. The relatively high sensitivity of Comperiella to low temperatures (threshold temperature of 15°C) (Auerbach 1984) may provide a partial explanation to the inability of this species to control the host during winter. A. chrysomphali, on the other hand, has a threshold temperature of 8.5°C, while the threshold temperature of A. melinus is

11°C (Abdelrahman 1974a). On the other hand, A. melinus is probably the fittest species for extremely high temperatures. The aggregation of Comperiella on fruits might indicate that this species is not distributed over the whole area of the host, while Aphytis species have a better distribution (e.g., Carroll 1979).

As shown in the present study, Aphytis coexists with Comperiella in the citrus groves of Israel. Although, theoretically Aphytis is a better competitor both internally and externally, the wider niche of Comperiella which attacks more developmental stages of the host, enables the two species to coexist, which also provides higher rate of overall parasitism than when any of these parasite species operates alone.

II. Chilocorus bipustulatus and C. kuwanae (Coleoptera: Coccinellidae). A comparative study.

-see papers appended at the end of this report (Podoler & Henen 1983, 1986 in the List of Publications).

III. The Florida wax scale and its natural enemies on citrus in Israel

The Florida wax scale (FWS), Ceroplastes floridensis Comstock (Homoptera : Coccidae), is an oviparous, uniparental, polyphagous soft scale insect, apparently of Oriental origin. It has been recorded from more than 70 host plants in Israel (Ben-Dov 1970). In the U.S. it occurs on about 25 host plants (Gimpel et al. 1974).

An economically important pest of many ornamental trees and shrubs, the FWS attacks citrus in at least 13 countries, causing varying degrees of economic damage (Talhouk 1975). It is a minor pest of citrus in Italy, Lebanon, Turkey, Florida, Brazil and Australia, whereas in Egypt, India, China and Mexico it is of intermediate importance. Israel appears to be the only country in which the FWS is a pest of major economic importance, where it is often the decisive factor in citrus pest management policy (Podoler et al. 1981). Recently, it has become a pest of growing economic importance in Greece (Argyriou & Kourmadas 1983).

The FWS has 3 larval instars (L1 - L3) and an adult stage which may be divided into young female (Yf), preovipositional (POf), and ovipositional (Of) female stages. - Two partially overlapping generations are produced annually in Israel. The spring generation begins in May - June and matures in August - September, whereas the fall generation begins in August - September and matures in the following spring. A third generation was recorded by Bodenheimer (1951) and Greenberg (1957).

Mortality is caused by climatic factors and the action of several natural enemies. Climatic factors, especially hot, dry winds (Hamsins) are considered important mortality factors in the crawler and first larval instar (Avidov & Harpaz 1969, Podoler et al. 1981). Natural enemies include predators, parasites, and an entomopathogenic fungus, Verticillium lecanii (Zimmerman) Viegas. Predators are mainly coccinellid beetles, of which Chilocorus bipustulatus (L.) is the most thoroughly studied species. This species prefers diaspidid prey, but has been shown to include crawlers and early stages of soft scales in its diet (Mendel et al. 1985).

Verticillium lecanii, used to control greenhouse populations of the brown soft scale, Coccus hesperidum L. (Homoptera : Coccidae), in the U.S. and England (Brady 1979), was found in field populations of C. floridensis in Israel (Kenneth et al. 1971). This fungus attacks all stages of the scale and is most prevalent in groves with above-canopy irrigation. In June, 1971, an epizootic was observed in the plain of Sharon (Kenneth & Olmert 1975). The occurrence of V. lecanii on FWS populations from the beginning of September through the winter months was noted as an unimportant mortality factor by Podoler et al. (1981).

The FWS has at least 10 primary and 4 secondary hymenopterous parasites in Israel (Rosen 1962, 1967, Ben-Dov 1970). Tetrastichus ceroplastae (Girault) (Eulophidae) was recorded to be the most prevalent species by Rosen (1967) and Ben-Dov (1972). Moranila californica (Howard) (Pteromalidae) was reported by Peleg & Kaminsky (1975) to be a significant mortality factor of the FWS in the Negev and Ashqelon, and it was also reported by Podoler et al. (1981) as the dominant parasite attacking FWS in Be'er Ya'aqov. A list of primary and secondary hymenopterous parasites is presented here:

Primary parasites:

Bothriophryne fuscicornis Compere (Encyrtidae)
Coccophagus lycimnia (walker) (Aphelinidae)
Diversinervus cervantesi (Girault) (Encyrtidae)
Diversinervus elegans Silvestri (Encyrtidae)
Metaphycus zebratus (Mercet) (Encyrtidae)
Microterys flavus (Howard) (Encyrtidae)
Moranila californica (Howard) (Pteromalidae)
Scutellista cyanea Motschulsky (Pteromalidae)
Scutellista nigra (Mercet) (Pteromalidae)
Tetrastichus ceroplastae (Girault) (Eulophidae)

Secondary parasites:

Cheiloneurus paralia (Walker) (Encyrtidae)
Marietta javensis (Howard) (Aphelinidae)
Pachyneuron concolor (Förster) (Pteromalidae)
Tetrastichus ceroplastophilus Domenichini (Eulophidae)

In Israel, parasitism is generally insufficient to suppress FWS populations below economic thresholds. FWS populations in Florida, however, are possibly held in check by parasites (Haman, personal communication). The objective of the present study was to determine the effect of parasites on FWS populations on citrus in Israel.

GENERAL METHODS AND MATERIALS

Four citrus groves were sampled in 3 geographic regions of Israel: two groves on the coastal plain - a Shamouti grove in Be'er Ya'agov and a Valencia grove in Rehovot; grapefruit groves in the Negev at Devira-Lahav and in the Yizrae'el valley at Sha'ar ha'Amaqim.

Each grove was sampled at approximately 2-week intervals. Be'er Ya'agov was sampled 23 times (17/8/80 - 8/8/82); Rehovot 9 times (27/7/80 - 23/11/80); Devira-Lahav 42 times (21/1/80 - 7/9/82); and Sha'ar ha'Amaqim 54 times (10/3/80 - 11/2/83). Some of the samples were removed from the trees and studied in the laboratory under a stereoscopic microscope. The remaining samples were observed on the trees with a hand lens, and data were read directly into a tape recorder.

Meteoreological data were obtained from nearby stations, 10 km. or less from sampling sites and in the same geographic region.

Field characters used to identify the developmental stages of the FWS are presented in Table 15.

The scale population was sampled, categorized into the stages described herein, counted and recorded.

Table 15. Field diagnostic characters used to identify the developmental stages of the Florida wax scale.

STAGE	SIZE (mm)	DIAGNOSTIC CHARACTERS
Egg	0.3 x 0.15	Pink or yellow, oval, smooth, shiny.
Crawler	0.35 x 0.2	Red-brown, dorsoventrally flattened, free moving.
L1	0.5-0.7 x 0.2-0.4	White dorsal wax cap divided into four distinct regions. White marginal filaments, not covered with wax.
L2	0.7-1.2 x 0.4-0.9	White dorsal cap fused. 15 distinct white marginal filaments. Red-brown space, between dorsal cap and base of marginal filaments, not covered with wax.
L3	1.0-1.5 x 0.8-1.1	White dorsal cap maximum size. Wet wax fills up space between dorsal cap and marginal filaments. This space turns from red-brown to white during this stage.
Yf	1.5-2.5 x 1.0-2.0	White dorsal cap distant from submarginal filaments which protrude upward. No evidence of space between dorsal cap and submarginal filaments.
POf	2.3-3.8 x 1.8-3.0	Maximum dimensions of width and length attained. Dorsal cap and marginal filaments are clearly evident.
Of	2.3-3.8 x 1.8-3.0	Scale growth in height, dorsal cap and marginal filaments are barely evident. Purple-white, wet wax covers entire dorsum, which becomes highly convex. Eggs are evident when the body is over turned.

Sampling the parasites - The objectives of sampling were to determine seasonal changes in percentage of parasitism (%P) and the effect of parasites on the FWS population. The host population sampled included all the developmental stages of the FWS which are susceptible to parasitism. For *T. ceroplastae*, which was the most abundant parasite found during the course of this study, the susceptible developmental stages are L3 - POf (Ben-Dov 1972). Samples were taken at approximately 2-week intervals. Three sampling methods were used: I. General random population sampling of the FWS, which usually yielded relatively small numbers of parasites. II. Separate sampling for parasitism made by walking up and down the rows of each grove,

covering as much area as possible and collecting branches and leaves with high host densities. III. In an attempt to eliminate biased samples and provide an additional measure of %P, five trees were selected randomly in each grove, using a table of random numbers. Each sample tree was divided into quadrants. Ten branches, each with five leaves, were randomly selected from each quadrant and brought into the laboratory. All samples were processed by cutting small pieces of leaf on which the scales were located, placing them in plastic cells (40x28x16mm), and rearing parasites at 27°C, 60% RH. In order to delay desiccation and prevent bacterial growth, a piece of filter paper treated with 0.15% chloramphenicol was placed on the bottom of each cell. The numbers of scales in developmental stages L3 _ POf and emergent parasites were recorded.

The keys published by Rosen (1966) were used to identify the parasites.

%P was determined by the ratio of number of parasites reared over the number of scales in the sample. Since T. ceroplastae is apparently a solitary parasite on the FWS, this ratio represented the actual %P (Rosen 1967).

RESULTS

The dominant parasite in the present study was T. ceroplastae, and this species is therefore the subject of analysis here. This parasite attacks both the FWS and the fig wax scale, Ceroplastes rusci (L.). It is apparently solitary in the former host, but two parasites have been observed to emerge from a single individual of the latter (Ben-Dov 1972). Other species reared from field samples included Tetrastichus ceroplastophilus, Scutellista cyanea and Moranila californica. The hyperparasite T. ceroplastophilus was second in order of abundance, whereas the other species were rare.

Seasonal abundance of T. ceroplastae - Seasonal variation in %P of FWS populations in 3 groves are presented in Figs 20-21. Spring and

fall peaks of %P are evident in all 3 groves. The spring peaks occurred in May - June and ranged from 12% to 50%; Fall peaks occurred in August - October and ranged from 2% to 37%. Spring peaks of %P corresponded to the appearance of susceptible hosts which were produced by the fall generation of FWS, and fall peaks of %P to the host's spring generation.

Figure 21. Seasonal changes in % parasitism by Tetrastichus ceroplastae, density of parasitized hosts (N_{ph}), and density of susceptible host stages (N_h) of the Florida wax scale, comparing two methods of data collection. Sha'ar ha'Amaqim.

Percentage of parasitism determined by general random sampling (method I) and by separate sampling (method II) are compared in Fig. 21 for the Sha'ar ha'Amaqim grove. The results from Devira-Lahav and Be'er Ya'agov are presented in Fig. 22.

The results obtained by these methods differ in the following respects. The first 3 peaks of method I are sharper and start slightly later than the peaks of method II. This can be explained by the fact that %P was largely determined by the number of post - parasitized hosts in method I, whereas later instars and pupal stages of the parasite also contributed to %P in method II.

Figure 22. Seasonal changes in % parasitism by Tetrastichus ceroplastae, density of parasitized hosts (N_{ph}), and density of susceptible host stages (N_h) of the Florida wax scale in A. Devira-lahav and B. Be'er Ya'agov.

The last group of peaks in method I represents parasites which were found dead within their hosts. These peaks were not evident in method II, since only emergence was recorded. Both methods have their advantages and disadvantages. Method I, while providing a non-biased sample, requires a greater sampling effort to obtain the same number of parasites. Method II was used for determining %P because it was based on greater parasite numbers and produced results comparable to those of the unbiased method. Sampling parasite populations by employing method III was carried out in 1982 in Sha'ar ha'Amaqim, and

the results were used to determine the relations between %P and host densities.

Seasonal variations in %P by T. ceroplastae in the present study were comparable with the results obtained by Rosen (1967), who recorded spring and fall peaks in April - June and September - October, and by Ben-Dov (1972), who recorded two well-defined peaks in April - May and July - August. %P values determined in the present study were also comparable to those cited by these authors.

Effect of parasites on host populations

METHODS

Methods of evaluating the effect of natural enemies on their host population are reviewed by DeBach (1964) and Kiritani & Dempster (1973). The method used in this study was based on life-table data (Varley et al. 1973). It involved determining the density of susceptible host stages (N_h) and of parasitized hosts (N_{ph}) on a generational basis. N_h was based on the number of scales entering the L3 - Yf stage category. Generational N_{ph} could not be directly assessed from the summation of successive values, nor could the peak value of %P, except under special circumstances (van Driesche 1983). Another method was therefore employed, based on the successive values of %P determined by method II and N_h determined by general field sampling. N_{ph} at each sample date was determined by multiplying %P/100 by N_h . Since N_{ph} includes hosts which may have been parasitized in previous sampling intervals, i.e., the same parasitized hosts could have been counted more than once; and since generations of the parasite (approximately 2 per host generation, see explanation below) could not be separated to construct life tables as was done for the host population; generational N_{ph} was calculated using a graphical method adopted from Southwood (1978). This method was carried out here by finding the area under the curve described by N_{ph} vs. degree-days above the parasite's developmental threshold, and dividing by the parasite's developmental constant. The threshold (7°C) and constant

(469 degree-days) for *T. ceroplastae* were published by Ben-Dov (1972). The maximum number of parasite generations per host generation (2.3) was calculated by dividing the number of degree-days required for development of susceptible host stages (1059 degree-days, from unpublished data by B. Schneider) by the parasite's developmental constant. The effect of parasites on their host population on a generational basis was expressed as the k value due to parasitism (k_p) where:

$$k = \log N_h - \log(N_h - N_{ph}).$$

RESULTS

The successive values of N_{ph} in three groves are illustrated in Figs. 20-21. Peaks of parasitism were usually separable and synchronized with spring and fall host generations.

Table 16. Parasitized host (N_{ph}) densities on a generational basis with the corresponding k_p value.

GENERATION	N_{ph}	N_h	k_p
	<u>Sha'ar</u>	<u>ha'Amaqim</u>	
S ¹ 1980	2	142	.01
F 1981	8	279	.01
S 1981	75	442	.08
F 1981	14	368	.02
S 1982	65	434	.07
F 1982	2	54	.02
	<u>Devira</u>	<u>Lahav</u>	
S 1981	24	221	.05
F 1981	18	438	.02
S 1982	141	1042	.06
	<u>Be'er</u>	<u>Ya'agov</u>	
F 1980	1	242	.002
S 1981	23	423	.02
F 1981	2	970	.0009

¹. S = spring; F = fall.

Parasitism of fall-generation hosts in Sha'ar ha'Amaqim consisted of 2 peaks. The first peak occurred toward the end of the fall, when

susceptible host stages were first being recruited, and the second in early spring. The first N_{ph} peak was due to a much lower %P than the second peak. The generational values of N_{ph} , N_h and k_p are presented in Table 16. Parasitism was not a significant mortality factor, since total mortality of the susceptible stages was much greater than that caused by parasitism.

DISCUSSION

Percentages of parasitism alone do not indicate the effect of parasite populations on their host populations (Bess 1945, van Driesche 1983). The use of life tables for determining the effect of different mortality factors on populations, traditionally used for studying human demography (Elandt-Johnson & Johnson 1980), has also been applied to insect populations (Bess 1945, Morris 1963, Dempster 1975, Varley et al. 1973). In the present study, the effect of T. ceroplastae in reducing FWS populations on citrus was found to be of minor importance. N_{ph} may have been underestimated, however, as a result of not taking into account the following: hosts which contained parasite eggs at sampling; hosts in which the parasite died, also killing the host; and parasitized scales falling off the tree. Another factor not taken into account which caused an underestimation of the effect of the parasite was host feeding (Ben-Dov 1972). Sublethal effects which reduce host productivity (DeBach 1964) may also play a role in the population dynamics of the FWS.

Relation between %P and N_h

METHODS

The relation between %P and host densities for field populations have been investigated by Embree (1966) and McClure (1977). This relation is a measure of the parasite's ability to respond to varying host densities and to regulate population densities. This relation was investigated in the present study by regressing %P on N_h between trees and tree sectors, using data obtained by sampling method III.

RESULTS AND DISCUSSION

The relation between %P and N_h on trees and tree sectors was investigated for 10 sampling dates. A significant relation was found in only one case between tree sectors. Observed and expected values of %P and N_{ph} vs. N_h for this relation are presented in Fig. 23.

Figure 23. The relations between %P (●=observed, ○=expected) and between parasitized host density (N_{ph}) (▲=observed, △=expected) vs. host density.

%P declined with increasing N_h approaching approximately 8%, and N_{ph} increased exponentially within the range of host densities found on this date. The effectiveness of *T. ceroplastae* was very low even when a significant relation between %P and N_h was found. The relation between %P and N_h was found to indicate the degree of parasite efficiency in two other field studies (Embree 1966; McClure 1977). In both cases, significant positive relations were found. Thus, 3 indications of the ineffectiveness of *T. ceroplastae* in reducing FWS populations in this study were: low rate of parasitism, small k_p values, and the absence of significant positive relations between %P and N_h .

SECTION 2. Research in California

Quantitative Evaluation of Natural Enemy Impact Against Homopteran
Pests of Citrus

Introduction

Integrated pest management is an ecologically based pest control strategy that relies heavily on natural mortality factors such as natural enemies and weather and seeks out control tactics that impede these factors as little as possible (Flint and van den Bosch 1981). Biological control is the foundation upon which this strategy is built and comes in several forms: (1) classical biological control which imports natural enemies usually for an exotic pest from its indigenous range, (2) augmentative biological control which supplements endemic natural enemies with periodic releases of insectary reared natural enemies, and (3) conservation of resident natural enemies by minimizing disruptive management practices (DeBach 1964, 1974, Huffaker 1971, Huffaker and Messenger 1976, Ridgeway and Vinson 1977).

Classical biological control has enjoyed a long and successful history beginning with the initial success achieved when the Vedalia beetle, Rodalia cardinalis, was introduced against the cottony-cushion scale, Icerya purchasi, in 1888. Between 15-19 percent of the classical biological control projects yielded complete and permanent control of the pest. Another 35 percent or so have yielded partial successes; that is they controlled the pest in part of its range or in some years but not in others. The remaining 45 percent or so were unsuccessful: either the natural enemies failed to become established or if they did

they failed to provide economic control (Laing and Hanai 1976, Hall and Ehler 1979, Hall et al. 1980). In most cases we do not understand why these projected succeeded or failed.

Augmentative releases, that is the practice of periodically releasing natural enemies to augment indigenous populations, has also been widely practiced and with some success. Nonetheless few of these programs are well documented and most are characterized by releases whose success vary unpredictably (DeBach 1964, Ridgeway and Vinson 1977). We understand very little about what makes a successful augmentative release agent or program.

Conservation of indigenous natural enemies is also a widely recommended practice in integrated pest management. Yet we do not know how to determine which indigenous natural enemies are effective and which are not. Nor do we understand under what circumstances can we expect a natural enemy to be effective.

A number of natural enemy attributes have been suggested as important in defining a successful biological control agent. These include (1) fitness and adaptability, (2) searching capacity, (3) power of increase relative to that of the host (prey), (4) host specificity and host preference, (5) synchronization with the host, (6) natural enemy aggregation at the denser host or prey patches, and (7) competitive ability (DeBach 1964, 1974, Huffaker et al. 1977, Hassell 1978, 1980, Waage and Hassell 1982). With the exception of host specificity and natural enemy aggregation at denser prey patches, these attributes are poorly defined or ambiguous. Moreover, few attempts have been made to

systematically test these assumptions and hypotheses using successful and unsuccessful agents from a successful biological control project. We have decided to do so and have chosen the California red scale as our model system.

We chose California red scale for several reasons: (1) the scale insect remains a serious pest of citrus in many arid and semi-arid regions of the world, (2) in California the history of its biological control is well documented - we know when and where the natural enemies were introduced and the consequences of these introduction, (3) natural enemies have been introduced that differ in their effectiveness ranging from those that failed to become established to those that provided effective biological control, and (5) the biologies of the scale and most of the natural enemies are well known. Thus we have an excellent system with which to determine what natural enemy attributes are responsible for the success or failure of an introduction and for the degree of biological control achieved (Rosen and DeBach 1978, 1979).

In California red scale occurs in the San Joaquin Valley of central California and the Coachella Valley (low desert), coastal areas and inland coastal valleys of southern California (Fig.24). All of these areas represent very different climatic regimes.

The red scale is multivoltine with an overlapping age structure. In California it has 2-4 generations depending on location and year. The degree of overlap amongst the various scale stages also varies as a function of location and season. Age structure patterns in red scale are important because the scale's parasitoid complex requires particular scale stages as hosts, principally 2nd and 3rd stage female and 2nd stage male scales. Figure 25 depicts the various red scale stages.

A number of natural enemies have been introduced into southern California as biological control agents of red scale prior to World War II but none proved effective (Rosen and DeBach 1978). However, DeBach did show that an ectoparasitoid, Aphytis chrysomphali, controlled the scale in the immediate coastal areas around Santa Barbara (DeBach and Sisojevic 1960). It had apparently been introduced along with the scale sometime before the turn of the century. This parthenogenic species occurred throughout the coastal and interior coastal valleys of southern California, but it was ineffective in all but the immediate coastal areas (Fig. 26).

In 1947, DeBach introduced a second Aphytis species, Aphytis lingnanensis, in an attempt to improve the biological control of red scale. It became established and excluded Aphytis chrysomphali from the interior valleys of southern California (Fig. 27). However, this species also proved to be largely ineffective in all but those areas along the southern California coast. Hence DeBach introduced a third Aphytis species, Aphytis melinus, in 1956-1957. This species quickly became established and displaced Aphytis lingnanensis from the more inland citrus areas of southern California (Fig. 28). Moreover, in most of these areas it provided excellent biological control (Rosen and DeBach 1978, 1979).

California red scale, although present in the San Joaquin Valley on dooryard citrus, had been largely excluded from commercial citrus by a practice of chemical eradication. It was not until the late 1960's and early 1970's that the scale moved into these groves. Unfortunately,

Aphytis melinus failed to economically control the scale in such groves even though it was generally distributed within the valley's citrus area (Flaherty et al. 1973, Luck and Warner, unpubl. data).

While monitoring the geographic spread of Aphytis melinus after its introduction DeBach noted that it was displacing Aphytis lingnanensis in the interior coastal valleys of southern California. In some cases this displacement took place even when the putative host stage for both these parasitoid species, virgin third stage scale, was abundant. Laboratory experiments in which DeBach investigated the competitive interaction between these two species led to confounding results: Aphytis lingnanensis, the losing species in the field, displaced Aphytis melinus in the laboratory. DeBach concluded, based on field evidence, that a shortage of third stage scale was not essential for competitive displacement and that, based on both laboratory and field evidence, Aphytis melinus won in competition with Aphytis lingnanensis because it was both a better searcher and better able to withstand temperature extremes (DeBach and Sundby 1963).

We have been unable to show any temperature differences between the two species large enough in effect to explain the displacement (Kfir and Luck 1979, 1984). However, in the course of conducting our experiments it became clear that DeBach's definition of the host stages used by each species was at odds with our observations. DeBach considered these wasps to be ecological homologues because they used the same host stages. We therefore conducted a set of host selection experiments in which we tested DeBach's hypothesis. The results of these experiments have been insightful. Not only have they suggested the basis for the

competitive displacement between the two parasitoid species, but they also suggested a hypothesis that might explain why Aphytis melinus was/is unable to control California red scale in the San Joaquin Valley. It is these results that I now relate.

Methods

. Haggai Podoler, Faculty of Agriculture, Hebrew University of Jerusalem, Rehovot, and I wished to know what types of scale served as hosts for these wasps. In particular we asked: what scale sizes did each parasitoid species use and how many eggs and of what gender did they allocate to them. We determined the sequence of behaviors associated with host selection in order to obtain a clear behavioral criterion that allowed us to determine when an egg had been laid without having to lift the scale cover (Fig. 29) (Luck et al. 1982).

Results

We found such a criterion: a pair of vibrations by the parasitoid marked the passage of the egg down the ovipositor. Moreover, we also gained an insight into the difference between gregarious behavior versus superparasitism in these species: if an individual is going to lay more than one egg on a host it remains on that host and repeats the sequence of behaviors (Fig. 29) for every egg it lays. This occurs in both species. However, once an individual walks off the scale cover it normally avoids laying additional eggs on that host. This is true for hosts previously parasitized by a congener as well as those parasitized by a conspecific. Our conclusion is that these parasitoids are able to evaluate the amount of available resources present in a host and to determine its value for producing offspring (Luck et al 1982).

Methods

Our conclusion that both Aphytis species evaluate the amount of resources present in a host is supported by our observations of parasitoid behavior obtained during the following set of experiments. We offered to individual female Aphytis melinus a range of scale size. About 20-40 third stage scale, the putative host for these parasitoids, were offered to each female and the size of parasitized and unparasitized scales were measured. We also transferred the young parasitoid larvae, individually, each to their own oleander scale. We transferred these larvae to exclude the possibility that differential mortality from insufficient food explained the differences in the host sizes from which male versus female offspring emerged. Each replicate had a range of scale sizes present but because of the scale's sessile habit we were unable to exactly duplicate the same size range in each replicate. Our results are summarized in Figure 30 (Luck and Podoler, 1985).

Results

The bottom graph (Fig. 30f) shows the range of scale sizes offered to the female parasitoids. The horizontal axis is scale size in square millimeters measured as the length times width of the scale's body. The vertical axis is the number of scales present in each size class. The second graph from the bottom (Fig. 30e) depicts the range of scale sizes parasitized. Two points are worth noting: first, the frequency of scale sizes parasitized was statistically the same as that offered and second, even though the hosts we offered were presumably all good hosts, 60% of them remained unused. The third graph from the bottom (Fig. 30d) depicts the scale sizes on which a single male parasitoid egg was laid,

the next graph (Fig. 30c) depicts the scale sizes on which a single female egg was laid, the next graph (Fig. 30b) depicts the scale sizes on which two eggs were laid. In every case one was a male and the other a female. And, finally, the top graph (Fig. 30a) depicts the scale sizes on which three eggs were laid. In all three cases they produced two females and one male. Also note the scale size at which Aphytis melinus begins producing female progeny, 0.39 sq. mm, and the scale size on which they begin to lay two eggs per host, 0.45 sq. mm.

Now compare these values to those for the scale sizes on which Aphytis lingnanensis begins to oviposit female (Fig. 31c) and multiple eggs (Fig. 31b). The data in these graphs (Fig. 31) were obtained using the same experimental design as that for Aphytis melinus. In all cases the scale sizes required by Aphytis lingnanensis are larger than those required by Aphytis melinus. We have conducted a number of similarly designed experiments and all of them show a similar relationship (Luck and Podoler, in press).

We can summarize our results in the following graph (Fig. 32). Both species oviposit male eggs on smaller hosts than female eggs and female eggs on smaller hosts than multiple eggs of mixed gender. The species, however, differ, in the minimum scale sizes on which they initiate this pattern: Aphytis lingnanensis requires larger scales than Aphytis melinus. But these are all laboratory data. What does this pattern mean in the field?

Here is the size distribution of third stage female scale on wood, leaves and fruit on grapefruit at Lod, Israel (Fig. 33). First note that the scales on wood are smaller than those on leaves and that the

scale on fruit are the largest. This pattern is statistically significant and has been previously reported by several researchers working with California red scale. Second, the arrows beneath the horizontal axis of each graph indicates the minimum scale size on which female progeny production was observed in the laboratory, the left most arrow for Aphytis melinus, the right most arrow for Aphytis lingnanensis. Third, the figures in the upper left-hand corner of each graph gives the percentage of the scale population on each substrate available to the two Aphytis species for female progeny production; the value to the left is for Aphytis melinus, the value to the right is for Aphytis lingnanensis. If the laboratory values for scale size on which daughters are produced is accurate then clearly Aphytis melinus has a larger proportion of the scale population available to it for the production of daughters (Luck and Podoler, in press).

Here is similar information on the size distribution of red scale on San Joaquin Valley navel oranges (Fig. 34). We see the same pattern of the smallest scale on wood, scale of intermediate size on leaves and the largest scale on the fruit. Note also the general shift of scale size to the left, that is the scales at this San Joaquin Valley location are relatively smaller than those on grapefruit in Lod, Israel. In general then we have found that scale size varies in a predictable way on the three substrates. It is always significantly smaller on wood than on either of the other two substrates and it is usually significantly larger on fruit than on any of the other substrates. However, the absolute scale size varies from one location to another in a way that we cannot predict.

Methods

Up to this point we have been talking about scale size based on laboratory experiments. In this graph (Fig. 35) the scale sizes used by Aphytis melinus in the field are presented. These data were obtained from scale populations infesting three cultivars at two locations in the Riverside, California area. Only those scales that had eggs or first instar parasitoids were measured as scales with older larvae had shriveled to the point where we were unable to measure their size with certainty. Again the size was measured as the length time width in sq. mm. Please note that the values on the abscissa should have decimal points preceeding them. We also transferred most of the larvae to large oleander scale to be certain that scale size was not affecting the gender of the emerging parasitoid through differential mortality. Note that both second instar, the dark bars, and third instar scales, striped bars, were considered as hosts (Luck and Yu, unpubl. data).

Results and Discussion

Clearly second instar scale are mostly a source of male parasitoids. Third instar scale are the primary source for female offspring. Note that the scale size on which female parasitoids are produced in significant numbers is about .38 sq. mm as compared to .39 sq. mm in our laboratory experiments. The six females we observed from the smaller scales appear to be nonfunctional based on Sue Opp's results (see Opp and Luck, in prep. - manuscript attached) in which she looked at female size and fecundity as a function of the scale size on which it grew. The multiple ovipositions are more difficult to interpret because multiple visits to a scale, i.e. superparasitism, cannot be excluded.

Thus gender allocation on scale in the field parallels the pattern we have observed in the laboratory. We have been unable to find an Aphytis lingnanensis population sufficiently dense to obtain similar data for this species although we are still looking.

On the basis of these and other data Dr. Podoler and I have hypothesized that Aphytis melinus displaced Aphytis lingnanensis in California because it used a smaller scale than Aphytis lingnanensis to produce daughters. Since a scale grows in size as it develops it enters the size range used by Aphytis melinus first. When an Aphytis parasitizes a host it paralyzes it, that is the scale is no longer able to increase in size. Moreover, Aphytis lingnanensis usually avoids ovipositing on previously parasitized hosts thus once Aphytis melinus parasitizes a host it effectively usurps that host as a resource and thereby prevents its use for progeny production by Aphytis lingnanensis.

Third stage females are the only resource on which Aphytis lingnanensis can produce daughters. This is also the principal resource for female progeny of Aphytis melinus as well. We thus looked at the variation in the abundance of third stage scale through the season.

This graph (Fig. 36) shows the relative abundance of second and third stage red scale at three sites in California: A somewhat coastal site, Fillmore, an interior coastal valley site, Riverside, and a San Joaquin Valley site, Exeter. At both Fillmore and Riverside the abundances of second and third stage scale vary. We suspect that this variation in scale abundance leads to periods in which suitable hosts for female progeny production are in short supply. However, third stage scale are reasonably abundant year round. The period during which

second and third stage scale were absent in 1982 at Fillmore was caused by a thrips treatment that interrupted the scale's age structure and caused substantial periods during which suitable Aphytis hosts were absent. This hiatus lasted longer than the 200 day degree life expectancy of an Aphytis adult. The scale population became economic.

Also note the pattern of relative abundance at Exeter. It shows substantial variation. This pattern is typical of San Joaquin Valley scale populations and it is this pattern that we suspect prevents Aphytis melinus from controlling California red scale in the valley. The periods during which suitable scale stages are absent or scarce are too long to allow many female Aphytis progeny to be produced and female Aphytis adults to survive. Thus too few Aphytis are about to parasitize the wave of suitable scale stages that follows the period of scarcity. We suspect winter temperatures synchronize the scale's age structure by inhibiting both insemination of virgin female scale and crawler production by parturient scale. We are seeking to test this and several other hypotheses with a combination of laboratory and field experiments should our BARD grant proposal be successful.

Finally, we come to the matter of field sex ration for Aphytis melinus. These data (Fig. 37) show the emerging sex ratio of wasp progeny individually isolated as immatures from monthly field samples taken during a six month period. Again notice that both male scales and second stage male and female scales were mostly a source of male wasps. Third stage scale were the predominant source for female wasps. But also note that in every sample the overall sex ratio was male biased and that this bias increased during the season (Luck and Yu, unpubl. data).

Thus the vast majority of parasite progeny produced are males and this occurred because the adult females parasitized mostly male and second stage male and female scales. This strongly suggests that the scale population was heavily exploited by the parasitoid. We observe this same pattern of male bias sex ratios in laboratory cultures when the parasitoid to host ratio is high and the scale population is heavily exploited. Thus all of our evidence to date strongly suggests that resource scarcity is the principal reason why Aphytis melinus displaced Aphytis lingnanensis in southern California and for the inability of Aphytis melinus to regulate red scale populations in the San Joaquin Valley at subeconomic densities.

With regard to the 7 attributes most frequently listed as characterizing a successful biological control agent most are too general to test with a specific system (e.g. fitness and adaptability) or too vague (e.g. searching capability: as with lingnanensis, the species may search more host habitat than A. melinus but it cannot use most hosts because they are too small). Others (e.g. host specificity) we have not tested yet or are currently analyzing (e.g. natural enemy aggregation at denser host patches). Three attributes we were able to test directly. Aphytis lingnanensis is the more fecund of the two species yet it could not realize this fecundity in as many daughters as A. melinus, so fecundity per se is not an important criteria relative to resource exploitation. We found synchronization to be a very important characteristic. Aphytis melinus requires a more or less continuous supply of third stage virgin females if it is to produce daughters. Interruption of this supply, i.e. variation in the age structure patterns of its hosts, longer than a critical period leads to uneconomic biological

control. Finally we can comment specifically on competitive ability. In our case it was the ability of A. melinus to produce daughters on a scale size (resource) that was smaller and scarcer than that required by A. lingnanensis. Although I expect this mechanism to operate in other systems, the particulars are likely to vary, thus each case involving competition is contextual and must be based on a firm understanding of what constitutes a host for each species and its value as a resource for progeny production.

We only uncovered these processes because we observed the host selection behavior of Aphytis melinus and Aphytis lingnanensis in detail. This technique allowed the parasitoid to tell us how it viewed its resources and how it used them. It is through such studies that we can begin to increase our understanding of biological control. I, therefore, urge its wider adoption as a research methodology.

ORANGE PRODUCTION DISTRICTS IN CALIFORNIA

Fig. 24. Citrus producing regions in California.

Fig. 25. California red scale stages. (1) Crawler (2) white cap
(3) 1st instar (4) 1st molt (5) 2nd instar (6) 2nd molt
(7) 3rd instar (virgin) (8) gravid (9) partuent
(10)

Fig. 26. 1948 Geographic distribution of *Aphytis chrysomphali* in southern California.

Fig. 27. 1961 Geographic distribution of *Aphytis chrysomphali*,
A. lingnanensis and *A. melinus* in southern California.

Fig. 28. 1965 Geographic distribution of *Aphytis chrysomphali*,
A. lingnanensis and *A. melinus* in southern California.

Fig. 29. Sequence of the behavior associated with host selection by Aphytis lingnanensis and A. melinus.

Fig. 30. The relationship between scale size (3rd instar California red scale) and the number and gender of Aphytis melinus eggs allocated to the scale.

Fig.3f. The relationship between host size and the number and gender of *Aphytis lingnanensis* eggs allocated to the scale.

Fig. 32. Summary of host size and the number and gender of eggs allocated to host by Aphytis lingnanensis and A. melinus.

Fig. 33. Frequency distribution of third stage scale sizes inhabiting wood, leaves and fruits of grapefruits growing at Lod, Israel.

Fig. 34. Frequency distribution of 3rd instar virgin California red scale on wood, leaves and fruit of Valencia oranges in the San Joaquin Valley of California.

Fig. 35. Relationship between scale size (California red scale) and the numbers and gender of Aphytis melinus eggs allocated to a scale at Corona and Riverside, California.

Fig. 36. Pattern of relative abundance of 2nd and 3rd stage California red scale at 3 California locations.

Fig. 37. 1983 Field sex ratios of *Aphytis melinus* at Corona and Riverside, California.

E. Description of Cooperation

Cooperation between the investigators involved in this project pre-dates this grant. Prof. Podoler spent a sabbatical at the Division of Biological Control, University of California, Riverside, at which time the research reported in the Luck et al. (1982) and a portion of the Luck & Podoler (1985) manuscript was conducted. The research reported in this last paper was completed under the auspices of the BARD grant. In addition, a project on sex of offspring and resource allocation by Pteroptrix smithi has been initiated during Dr. Luck's visit to Israel (April - June, 1982), supported by the BARD grant. Thus, the emerging pattern and understanding of resource utilization by scael-insect parasitoids and its consequences for biological control is a result of the long-standing efforts by these investigators.

F. Benefits to Agriculture

Insect natural enemies are a pervasive feature of most phytophagous insect systems. Many of them are known to be responsible for controlling host or prey populations. Insect pest management is founded on this notion and advocates preserving and manipulating these entities to achieve control, yet we know little about what constitutes an effective natural enemy. Our research seeks to increase this knowledge by comparing complexes of natural enemies, both effective and ineffective, from successful biological control programs to define those attribute that characterize an effective natural enemy.

The results obtained by the Israel group have indicated that tolerance to high temperatures and pesticides may be critical factors determining the establishment and efficacy of natural enemies and the composition of natural-enemy complexes.

The California group's results have identified two important factors: resource quality (size of the host insect) and availability. These results have also suggested guidelines for mass rearing of several natural enemy species and for evaluating conditions when resident

natural enemy populations are inadequate and should be augmented with insectary-reared individuals.

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M.Sc. Theses

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Ph. D. Thesis

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