

Role of natural enemies and other factors in the dynamics of field populations of the whitefly *Siphoninus phillyreae* (haliday) in introduced and native environments

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Abstract

The parasitoid wasp *Encarsia inaron* was introduced from Israel into the US and led to successful biological control of the whitefly *Siphoninus phillyreae*. The whitefly and its parasitoids were studied in the laboratory and the field in Israel. The results provided additional insight into the process of natural enemy selection for biological pest control. They enabled comparison of (i) whitefly and parasitoid biology and (ii) the role of *E. inaron* in host population suppression in the two countries. Natural enemies of *S. phillyreae* other than *E. inaron* are uncommon in Israel. Laboratory results for *S. phillyreae* were: mean (\pm SE) developmental time 23.3 (\pm 16) days; female longevity 26.5 (\pm 0.3) days; fertility 118 (\pm 9.6) eggs/female; and survival from egg to adult 41%. For *E. inaron*, mean (\pm SE) developmental time was 20.0 (\pm 0.6) days and net reproductive rates of ca. 11.5 early in the season and 0.2 in September/October. These findings sufficiently resembled those for *S. phillyreae* and *E. inaron* in California, to permit comparison between the two systems. In Israel, whiteflies were most abundant in August and their egg to adult survival declined from 19% in May and June to 0.4% in September and October. Unassigned loss of young whitefly nymphs was the largest single mortality factor while mortality caused by *E. inaron* ranged between 24 and 78%, occurring in both low and high host populations. We discuss the usefulness of parasitoid performance attributes in its country of origin, for the selection of parasitoids for biological control programs.

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1. Introduction

In biological control, exotic natural enemies often are introduced from one place to another to effect pest suppression (Van Driesche and Bellows, 1996). This is based on the premise that discovering, importing and colonizing natural enemies that occur where an insect is not considered a pest will bring it under control in the country of introduction. Thus, we must first discover the appropriate natural enemies that, once properly introduced into another host-infested habitat, will effectively control that host. This theory has been frequently tested

and proven ever since the introduction of the Vedalia beetle [*Rodolia cardinalis* (Mulsant)], first into California in 1898 and then into many other countries (see DeBach and Rosen, 1991, for a review). However, DeBach and Rosen (1991) also noted that: “the ultimate success of a given natural enemy candidate for importation cannot be predicted in advance.” Other workers (e.g., Ehler, 1990; Van Driesche and Bellows, 1996; Waage, 1990) suggest that the selection of efficacious natural enemies can be based on a group of ecological and behavioral criteria. These criteria, which constitute our main tool for selecting appropriate natural enemies, are continually being examined and improved, based on past experience and advances in ecological theory (e.g., Murdoch, 1990; Stilling, 1993).

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Development of more precise criteria has been hampered by the lack of biological and economic evaluations of both successful and unsuccessful attempts at biological control. The reasons for this lack often related to a misunderstanding of the importance of such work (Waage, 1990). Moreover, even projects that have been evaluated are usually confined to the characteristics of the natural enemy either in the laboratory or in the areas of introduction. As far as we are aware, no attempt has been made to examine the role of the natural enemy in its endemic range after it has proven successful as an introduced control agent. Such a study, an a posteriori examination of the biological attributes of a successful natural enemy, could serve as a testing ground for the current selection criteria and may also provide new ones.

The ash whitefly, *Siphoninus phillyreae* (Haliday) is known throughout much of the subtropical and temperate eastern hemisphere, from the Indian subcontinent, through the Middle East, to the European and African regions of the Mediterranean, north to Poland and south into tropical Africa (Bellows et al., 1990). In most of these regions it is not currently reported in the literature as a pest, and has rarely achieved pest status. A number of natural enemies are recorded throughout its range, including several parasitoids and a few predators (Bellows et al., 1990).

Siphoninus phillyreae was introduced into California sometime prior to July 1988, when it was discovered infesting at least 4000 km² in Los Angeles County. Within the following few months it had spread to cover 32 counties in California as well as portions of Nevada, Arizona, and New Mexico (Bellows et al., 1990). It reached extreme densities, with nymphal populations occupying >80% of the available foliage of susceptible host plants (Bellows, unpublished). The extreme density of aerial populations led to the cessation of normal human outdoor activities (Bellows et al., 1990). Its host-plant range included more than 50 species of plants in 11 families (Bellows et al., 1990). Large populations defoliated susceptible shade and fruit trees, and repeated defoliations led to the death of some trees and severely reduced production in others.

In response to this infestation, a biological control program against *S. phillyreae* was initiated at the University of California in Riverside. Selection of natural enemies followed the common guidelines for such cases (e.g., Bartlett and van den Bosch, 1964). In this case it was simple to find locations in which *S. phillyreae* occurred but was not pestiferous, since that was the situation in most of its known range. Parasitized host material was imported, among others, from Israel and southern Italy, whose climates resemble that of the regions of California in which the pest occurred. The Israeli material included *Encarsia inaron* (Walker) [as *Encarsia partenopea* Masi] that had been developing in *S. phillyreae* on pomegranates near Tel Aviv, and the

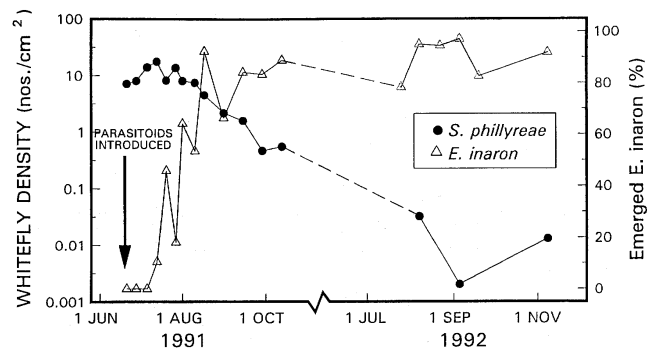


Fig. 1. Biological control of *S. phillyreae* by *E. inaron* Walker in California (after Bellows et al., 1992).

coccinellid *Clitostethus arcuatus* (Rossi), while the Italian material included *E. inaron* from a laboratory culture at the University of Naples in Portici. Releases into California included *E. inaron* from Italy in San Diego County, *C. arcuatus* in several counties (excluding Riverside), and *E. inaron* from Israel (throughout California except San Diego County). The impact of the introduction of the Israeli wasp was studied in greatest detail in Riverside County. Populations declined over four orders of magnitudes within 18 months, in the presence of only the Israeli parasitoid (Fig. 1) (no native parasitoids adopted the whitefly as a host). During the initial population increase of the parasitoid following its release, parasitism rates exceeded 95% (Bellows et al., 1992; Fig. 1), but subsequently (at lower population levels) decreased (Gould et al., 1992). The new population density of the pest has remained extremely low for several years (Bellows, unpublished), and the whitefly is now found only on a few highly suitable host plant species in low numbers. The whitefly has since also been recorded from Chile, Mexico, and New Zealand, and the parasitoid has now been distributed to these regions.

This successful biological control campaign and the life table analysis that accompanied it (Gould et al., 1992) were followed by a study in Israel that quantified aspects of the population dynamics of *S. phillyreae* in the field, with special emphasis on the role of different mortality factors upon its populations. These two studies enable comparison of the role of known natural enemies in the home country of the pest and at the site of their introduction.

2. Materials and methods

2.1. General

Two species of host plants were used for the whitefly culture: an ornamental evergreen variety of ash (*Fraxinus* sp.) and pomegranate (*Punica granatum* L.). The former was used for the maintenance of winter cultures and for whitefly oviposition experiments, while the

latter, which is the most common host of *S. phillyreae* in Israel, was used for the developmental duration experiments and for general culture. Plants were potted in buckets and kept in a non-heated greenhouse during the winter and in an open court from spring to fall.

Whiteflies were collected as pupae in the field continuously from July, and kept in petri dishes until adult emergence. The adults were placed on host plants on which they grew from then on. Cultures were kept both in the laboratory in environmental cabinets ($30 \pm 2^\circ\text{C}$, 14/10 L/D, 60% RH) and in an open court. Parasitoids were collected in the laboratory as they emerged from whitefly pupae and were placed on infested plants, which were kept either in separate environmental cabinets, or in large organandy-walled cages.

2.2. Laboratory observations

Developmental durations of both *S. phillyreae* and *E. inaron*, and preimaginal survival of *S. phillyreae*, were studied in the environmental cabinets. For *S. phillyreae*, a pomegranate plant was placed in the cabinet into which adult whiteflies were released 1 week later. The adults were removed after 24 h and the plant leaves examined for whitefly oviposition. Seven egg-bearing leaves were marked, and the numbers and stages of the whitefly nymphs that were growing on them were recorded daily, using a stereomicroscope, until completion of adult whitefly emergence.

Parasitoid development was studied on infested ash leaves, whose large size facilitates observation of parasitized whiteflies. Infested plants were kept until the whiteflies reached the third nymphal instar, when they were exposed to 2–5 *E. inaron* females for 48 h. The parasitized whitefly pupae were observed daily and the date of adult emergence was recorded.

2.3. Outdoor observations

The number of eggs per *S. phillyreae* female was monitored by confining 23 freshly emerged (up to 16 h old) females in individual clip cages on pomegranate leaves. A male was added to each cage at the onset of observations. Females were observed each day and, if still alive, were moved with the cage to a new leaf after an interval of 9–12 days. The total number of eggs laid in each interval was registered. Dead females were removed and the number of eggs laid since the end of the last interval was recorded.

Sex ratios of both whiteflies and parasitoids were determined by collecting leaves bearing pupae in the field and keeping them in petri dishes until emergence was completed. The sex of the dead adults was determined and the ratio of females to males was calculated.

Estimations of relative whitefly population levels in the field were conducted by employing a fixed-time

search method. Pomegranate leaves were turned over and observed, and the findings were read aloud to a second person who registered them. The presence of any trace left by *S. phillyreae*, such as waxy spots, eggs, or nymphs, was counted as a positive incident. A 1-h observation was carried out once each month from May through August. Mortality-factor analysis was done during 1991 on Tel Aviv University campus through daily observations of naturally infested pomegranate trees in four locations. In three locations, observations started in early April and ended on 25 October. Another, fourth location was added on 28 July and observations continued till 16 September. Data collected during this period were grouped into four sets, each approximately one generation in length: one containing the combined observations from May and June, one each from July and from August, and one combined from September and October. Trees were examined for leaves bearing fresh whitefly oviposition, recognizable by its light color. Each infested leaf was marked by a ribbon tied near it bearing the date and serial number of the leaf. From that day on, the whitefly nymphs on the same leaves were observed regularly, with the aid of a magnifying glass, until the nymphs had pupated. The leaf with the pupae was then transported to the lab, where the adult whiteflies and/or parasitoids were allowed to emerge. Whitefly exuviae were classified as having either healthy whiteflies or adult parasitoids emerge from them. Examination took place daily until July, when the whitefly population increased; thereafter it was conducted once every 3–5 days. Data recorded daily from each observed leaf included the number of whitefly eggs, or third and fourth instar nymphs, and all predacious insects. First and second instar whitefly nymphs were not registered, because they were not readily visible with a magnifying glass and their counts proved to be unreliable. A total of 277 leaves were marked and observed during the season.

2.4. Analyses

From the counts of whitefly eggs, nymphs, and the number of emerged adult whiteflies and parasitoids, we constructed life tables (Bellows et al., 1990), incorporating Elkinton et al.'s (1992) calculation for marginal mortality rates of contemporaneous factors to quantify the relative impact of parasitism and other mortality factors. Since third instar nymphs are not transparent and did not enable us to determine their parasitism rates and since all parasitoids that survived emerged from fourth instar, we assigned all parasitism to that stage. This was then examined by calculating the marginal mortality rates caused by parasitism (Fig. 5). Estimation of predator activity was done by multiplying the number of predators found on each leaf by the number of days of their presence. The resulting 'predator-days' unit enabled comparison of the activity periods of the different

predators with each other and with the levels of whitefly populations throughout the season.

Sex ratios were compared using χ^2 tests. Variations in population means were expressed as the standard error of the mean (\pm SE). Relationships between various mortalities and whitefly density were tested using regression analysis. Calculations were performed on a personal computer running SAS GLM software (SAS Institute, 1988).

3. Results

3.1. Adult longevity, fertility, preimaginal development, and sex ratio

Survival of *S. phillyreae* adults under protected outdoor conditions ranged from 10 to 40 days (Fig. 2), with

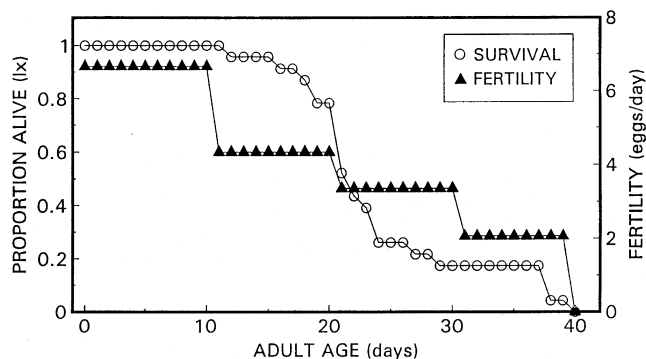


Fig. 2. Adult longevity and fertility of *S. phillyreae* on *P. granatum* in Tel Aviv.

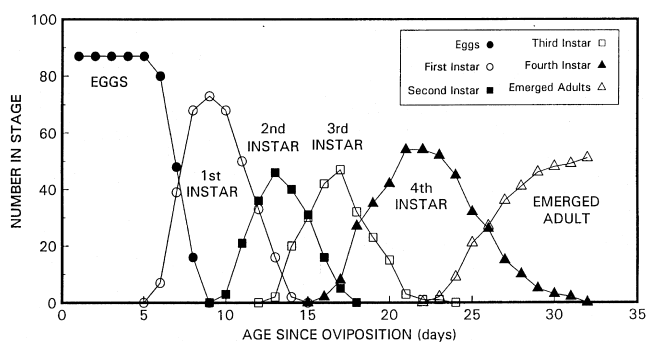


Fig. 3. Partial population curves for development of a cohort of *S. phillyreae* on *P. granatum* at 30 °C.

mean longevity of 23.3 ± 1.6 days ($N=23$). Fertility was highest (approximately 7 eggs/day) in the first recording period (Fig. 2), and diminished in each succeeding period until reaching approximately 2 eggs/day near the end of the maximal longevity. Total fertility was 117.8 ± 9.6 eggs/female.

Preimaginal development of a cohort of eggs varied, so that eggs hatched over a 4-day period. Subsequently, development through the remaining instars added slightly more variance, and emergence as adults occurred over a 10-day period (Fig. 3). Median developmental time from egg to adult was 26.0 days ($N=51$) (mean 26.5 ± 0.3 days, mode 25 days). Longest developmental times among the various stages occurred in the egg and fourth nymphal instars stages (Table 1).

Preimaginal developmental times for *E. inaron* spanned 16–32 days, and were probably dependent to some degree on the developmental time of the individual whitefly hosts as shown by Gelman et al. (2001) for *Encarsia formosa* Gahan. Median developmental time was 20.0 days ($N=54$), (mean 21.1 ± 0.6 days, mode 17 days). The second to early fourth instar host nymph (stages susceptible to parasitism) were present for approximately 11 days in the cohort developmental study (Fig. 3), indicating that there would be ample overlap in parasitoid and host developmental times for contemporaneous or synchronous development of the host and parasitoid population.

Preimaginal survival of *S. phillyreae* under laboratory conditions varied among stages (Table 2). Of 87 recorded eggs, 51 emerged as adults. The greatest mortality occurred between egg and first instar (16%) and between first and second instar (16%), accounting for most of the overall 41% mortality. Mortality in the other nymphal instars was smaller, varying from 3 to 7% (Table 2).

The sex ratio of *S. phillyreae* on 48 of the 49 collected leaves was not different from 1:1 (109 females and 93 males, $\chi^2=1.27$, OSL=0.260). On one exceptional leaf, a total of 25 females and 8 males emerged. If the results from this leaf are combined with those from the other leaves, the overall sex ratio is 1.14 females to 1 male, or 57.0% female. While this ratio is significant ($\chi^2=4.63$, OSL=0.031), we considered it rare enough to use a sex ratio of 1:1 in the remainder of our calculations that require this parameter in our study. The collections for *E. inaron* yielded 559

Table 1
Preimaginal developmental time for *S. phillyreae* reared on *P. granatum* at 30 °C

| Stage | Median developmental time (days) @ 30 °C (this study) | Median developmental time (days) @ 25 °C (Leddy et al., 1995) | Median developmental time (days) @ 30 °C (Leddy et al., 1995) |
|--------------------------------------|---|---|---|
| Egg | 7.6 | 8.95 | 8.75 |
| First instar nymph | 5.0 | 2.66 | 3.202 |
| Second instar nymph | 2.7 | 3.14 | 2.91 |
| Third instar nymph | 3.6 | 3.654 | 2.91 |
| Fourth instar nymph | 7.3 | 9.405 | 7.34 |
| Total preimaginal developmental time | 26.0 | 27.68 | 24.3 |

Table 2
Preimaginal mortality of *S. phillyreae* reared on *P. granatum* in the laboratory

| Stage | Age specific survivorship l_x | Age specific mortality d_x | Apparent mortality q_x | Real mortality in stage d_x |
|---------------------------|---------------------------------|------------------------------|--------------------------|-------------------------------|
| Egg | 87 | 14 | 0.161 | 0.161 |
| First | 73 | 12 | 0.164 | 0.138 |
| Second | 61 | 2 | 0.0328 | 0.0230 |
| Third | 59 | 4 | 0.0678 | 0.0456 |
| Fourth | 55 | 4 | 0.0727 | 0.0460 |
| Overall survival Adult | 51 | | | 0.5863 |

Table 3
Values of reproductive parameters for *S. phillyreae* from different laboratory studies

| Parameter | Source | | |
|-------------------------|---------------------------------|---|---|
| | This study @ 30 °C ^a | Leddy et al., 1995 @ 25 °C ^b | Leddy et al., 1995 @ 30 °C ^b |
| Preimaginal survival | 0.5863 | 0.6900 | 0.2398 |
| Fertility (eggs/female) | 118 | 141 | 66.6 |
| Sex ratio | 0.5 | 0.5 | 0.5 |
| R_0 | 34.6 | 48.6 | 7.98 |
| T_c | 37.0 | | |
| r_m | 0.1026 | | |

^a On *P. granatum*.

^b On *Fraxinus* sp.

males and 610 females (52.1% female), a ratio not significantly different from 1:1 ($\chi^2 = 2.22$, OSL = 0.136).

The preimaginal survival rate, fertility schedules and sex ratio on *P. granatum* were used to provide estimates of net reproductive rates for this population under our laboratory conditions (Table 3). The population yielded a reproductive rate of 34.6 times per generation, a value between the reproductive rates reported by Leddy et al. (1995) at 25 and 30 °C on *Fraxinus uhdei* (Wens.).

3.2. Field data and life tables

Leaf counts indicated that whiteflies were uncommon in the early part of the season, when an average of approximately four infested leaves was found per 10-min count (Fig. 4). Populations increased through July and August, and recorded densities increased to nearly 60 infested leaves per 10-min count.

Overall survival from eggs to adults recorded on infested leaves generally declined during the season from approximately 19% in May and June to below 1% in September and October (Fig. 4, Table 4). The life table analysis (Table 4) indicates that unidentified loss of whitefly nymphs was the largest mortality factor in nearly every seasonal interval and every stage, with stage-specific marginal mortality rates of 56–89% for the egg to second nymphal instar stages, 9–31% for the third nymphal stage, and 32–91% for the fourth nymphal stage. This unassigned loss increased generally throughout the season (Fig. 5). Mortality assigned to the parasitoid *E. inaron* (during the fourth nymphal instar when the parasitoid emerged as an adult) ranged from 24 to 78%. Parasitism was clearly not a key mortality factor *sensu*

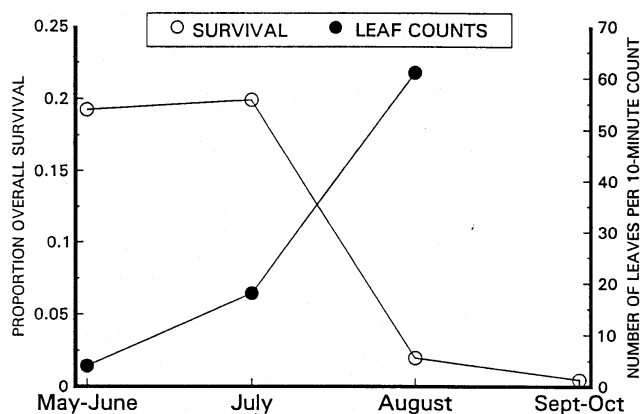


Fig. 4. Numbers of infested leaves found per 10-min count and proportional overall survival of *S. phillyreae* on *P. granatum* L. in the field in Tel Aviv.

Varley and Gradwell (1968), as its seasonal pattern among the four periods (Fig. 5) was not similar to overall mortality. Indeed, if a key factor could be determined from these data, it would be that of unassigned mortality in the egg-to-second nymphal instar period. Generally, the greatest mortality over the season was unassigned mortality in the egg-to-second nymphal stage.

We combined the overall mortality recorded in these four periods with the previously recorded fertility and sex ratio to calculate net rates of increase for this population across the season (Table 5). In the May–June and the July periods, rates of increase were relatively high (11.4 and 11.7 times per generation, respectively), reaching nearly 33% of the rate measured in the laboratory. In August, the rate declined to 1.2 times per generation and in September–October it was 0.3, well below the level

Table 4
Life tables for *S. phillyreae* on *P. granatum* in the field during May–June, July, August, and September–October in Tel Aviv

| Stage | l_x | Factor | Per factor d_x | Per stage d_x | Marginal mortality rate |
|---------------------|-------|------------------|------------------|-----------------|-------------------------|
| May–June | | | | | |
| Egg | 156 | Unassigned | 90 | 90 | 0.5769 |
| Third instar nymph | 66 | Unassigned | 6 | 6 | 0.0909 |
| Fourth instar nymph | 60 | | | 30 | |
| | | <i>E. inaron</i> | 13 | | 0.2595 |
| | | Unassigned | 17 | | 0.3248 |
| Adult | 30 | | | | |
| July | | | | | |
| Egg | 1970 | Unassigned | 1112 | 1112 | 0.5645 |
| Third instar nymph | 858 | Unassigned | 81 | 81 | 0.0944 |
| Fourth instar nymph | 777 | | | 385 | |
| | | <i>E. inaron</i> | 158 | | 0.2448 |
| | | Unassigned | 227 | | 0.3320 |
| Adult | 392 | | | | |
| August | | | | | |
| Egg | 1212 | Unassigned | 834 | 834 | 0.6681 |
| Third instar nymph | 378 | Unassigned | 65 | 65 | 0.1720 |
| Fourth instar nymph | 313 | | | 289 | |
| | | <i>E. inaron</i> | 168 | | 0.7753 |
| | | Unassigned | 121 | | 0.6588 |
| Adult | 24 | | | | |
| September–October | | | | | |
| Egg | 1081 | Unassigned | 957 | 957 | 0.8853 |
| Third instar nymph | 124 | Unassigned | 39 | 39 | 0.3145 |
| Fourth instar nymph | 85 | | | 80 | |
| | | <i>E. inaron</i> | 12 | | 0.3462 |
| | | Unassigned | 68 | | 0.9100 |
| Adult | 5 | | | | |

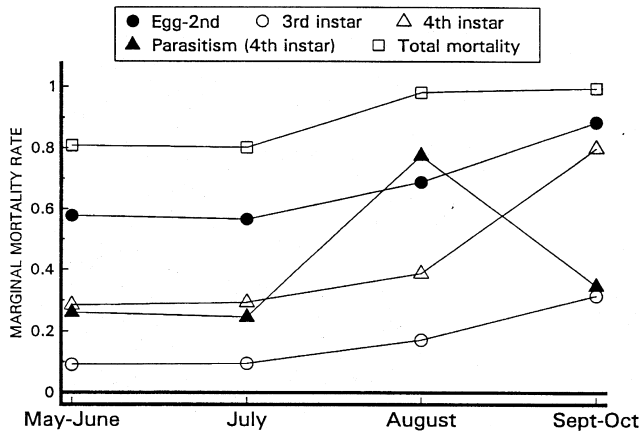


Fig. 5. Unassigned mortality during egg-second nymphal instar period, third nymphal instar period, and fourth nymphal instar period, and marginal rate for parasitism of fourth instar nymphs for *S. phillyreae* on *P. granatum* in the field in Tel Aviv.

required to maintain the population. We can examine directly the effect of the parasitoids on these reproductive rates by removing parasitism from the life tables and recalculating the net reproductive rates. These adjusted reproductive rates show that the proportional changes with vs. without parasitism (Table 5) were similar among

the three monthly groups: May–June–August, ranging from a difference in the R_0 values of 3.81 (July) to 4.03 (August).

3.3. Density dependence and related analyses

We considered further the data collected for each of the 277 leaves examined in the field in order to address two particular questions: (1) can we relate the unassigned mortality to the presence or activity of either predators or parasitoids, and (2) were there density-dependent relationships in the presence or action of predators or parasitoids, or in unassigned mortalities?

To address question 1, first we noted that predators were not uniformly present during the season (1.31, 0.56, 0.59, and 0.02 predator days/leaf for May–June, July, August, and September–October, respectively). This is in contrast to the seasonal pattern of unassigned mortality (Fig. 5). Of the predators recorded (Table 6), the majority of predator-days were the result of the presence of larvae of the coccinellid *C. arcuatus*. Most predators were observed only on 1 or a few days. One larva of *Acletoxenus* sp. (Diptera) was present on a leaf for 16 days.

The relationship between overall unassigned mortality (for each individual leaf) and the number of predator-days

Table 5

R_0 calculated as the product of proportional survival across the season (from field studies), sex ratio (0.5), and fertility (from laboratory studies) for *S. phillyreae* on *P. granatum* in the field in Tel Aviv

| | Period | | | |
|---|----------|--------|--------|-------------------|
| | May–June | July | August | September–October |
| With parasitism | | | | |
| Preimaginal survival | 0.1923 | 0.1990 | 0.0198 | 0.00463 |
| Sex ratio | 0.5 | 0.5 | 0.5 | 0.5 |
| Fertility | 118 | 118 | 118 | 118 |
| R_0 | 11.35 | 11.74 | 1.168 | 0.273 |
| Recalculated without marginal rate for parasitism | | | | |
| Preimaginal survival | 0.2597 | 0.2635 | 0.0881 | 0.00708 |
| R_0 | 15.32 | 15.55 | 5.199 | 0.4175 |

Table 6

Presence of predators on *S. phillyreae*—infested leaves of *P. granatum* in the field in Tel Aviv

| Predator | No. of predators observed in period | | | | Total | Total predator-days ^b |
|--|-------------------------------------|------|--------|-------------------|-------|----------------------------------|
| | May–June | July | August | September–October | | |
| <i>C. arcuatus</i> adults ^a | | 3 | 2 | 1 | 6 | 6 |
| <i>C. arcuatus</i> larvae | 2 | 12 | 15 | | 29 | 99 |
| Other adult Coccinellidae | 4 | | | 1 | 5 | 5 |
| Larval Coniopterigidae | 2 | | | | 2 | 2 |
| <i>Acletoxenus</i> sp. larvae | | 1 | | | 1 | 16 |
| Lepidopteran larvae ^c | | 2 | | | 2 | |

^a Coleoptera: Coccinellidae.

^b Total number of individuals observed times the number of days they were present.

^c Lepidopteran larvae fed on the infested leaves, not directly on the whiteflies, and were not included in the predator-day calculations.

and between unassigned mortality and the marginal mortality rate of parasitism was also examined. Although both regressions had slight positive slopes, neither was significant. We concluded that these data did not indicate a relationship either between the presence of predators or activity of parasitoids and unassigned mortality.

To address question 2 (examining mortality rates for density dependence), our analyses included regressing marginal mortality rates against density of the stage upon which it acted (i.e., unassigned [unexplained] mortality in the third instar vs. third instar density) (Fig. 6). In these independent observations on leaves, there is no temporal interdependence in the data. These regressions are, however, imperfect in that they are subject to the normal biases present when proportional data of random variates (such as mortality rates) are regressed against the denominator of the proportion. This bias would tend to make the regressions slightly more negative than they should be under the null hypothesis of no density relationship. We know of no practical means of avoiding this bias, but note that the biases are likely to be small.

The unassigned mortality rates during the egg to second nymphal instar period varied widely (from 0 to 1) and showed no apparent relationship to egg density, and indeed its regression against egg density was not significant. The regression of unassigned mortality in the third and fourth nymphal instars (here grouped as a single

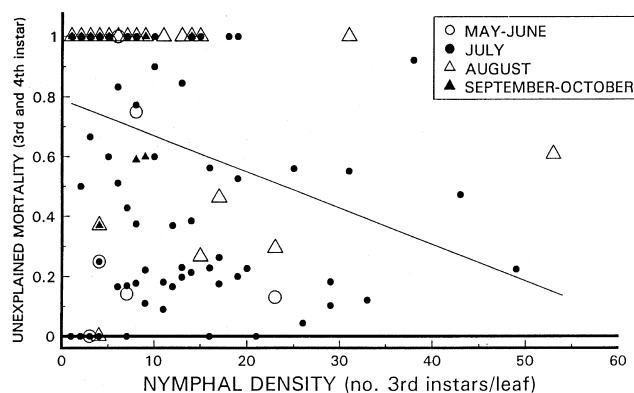


Fig. 6. Unassigned (unexplained) mortality in third and fourth instar nymphs vs. nymphal density ($y = 0.790 - 0.0121x$, $r^2 = 0.077$, $F = 13.67$, $OSL = 0.0003$).

stage) against third instar density was significantly negative ($OSL = 0.0003$) (Fig. 6). It reflects a large number of leaves with relatively few (fewer than 15) nymphs where no nymph survived to the adult stage. This mortality rate was thus inversely density dependent.

The action of parasitoids in the system was considered in two steps: (1) presence of a parasitoid on a host-infested leaf and (2) successful parasitization of the hosts on that leaf. To examine the first process, we grouped leaves in geometric ranges of third instar nymphal density and calculated the proportion of these leaves, which were known to have been discovered by a parasitoid as

evidenced by the presence of parasitized whiteflies. This relationship was significant: leaves with greater host densities were more likely to yield one or more parasitoids ($y = 0.0879x + 0.0412$; $R^2 = 0.7736$). Over the range of host densities in the study (1–54 third instar nymphs/leaf), the likelihood of recovering a parasitoid from leaves increased from zero to over 66%. Overall, a total of 66 of the 277 leaves yielded parasitoids (23%).

Regressions of parasitism rate on each leaf (marginal mortality rates for parasitism) against density (either third nymphal instar density or egg density) on individual leaves were not significant. Parasitism rates were highly variable even for leaves with similar host densities. Hence in this system, whether or not a leaf yielded parasitoid progeny was a density dependent process, but the rate of mortality imposed by a parasitoid on a discovered leaf does not appear to have been related to the density of hosts on the leaf.

The likelihood that a leaf would bear a predator was also related to host egg density ($y = 0.0429x - 0.0833$; $R^2 = 0.867$). The total number of leaves on which a predator was observed was 11.9% (33 of the 277 leaves).

4. Discussion

The study was aimed at testing whether the biological control potential of an introduced natural enemy could be inferred from its life history traits in its area of origin. We used as a test case the recent biological control of *S. phillyreae* in California by the natural enemy *E. inaron* introduced from Israel. In California, this wasp alone was responsible for a reduction in density of over four orders of magnitude throughout the infested region, and is now being employed in other areas in North America as well as in New Zealand and South America.

As background to our study, we first examined the biology of the whitefly host in Israel, noting that the origin of the whitefly population introduced into California is unknown. Comparing the biology of the Tel Aviv and California populations revealed the similarities/differences of these two populations. Mean adult longevity and median developmental duration from egg to adult (Table 1) in the Tel Aviv population growing on *P. granatum* were slightly, but not significantly, longer (23.3 vs. 19.7 and 26 vs. 24.3 days, respectively) than the California population reared on *Fraxinus* sp. (Leddy et al., 1995). Fertility was greater in the California population at 25 °C (141 eggs/female, Leddy et al., 1995), but was lower at 30 °C (66.6 eggs/female). Survival from egg to adult in the laboratory was 58.3% in Israel (the present study), and 66.0% at 25 °C, and 24.0% at 30 °C in California (Leddy et al., 1995). These differences may partly represent the effects of the two different host plants used in the two studies, or the different response of the plants to the fixed temperature (and thereby their suitability as

a host plant to the whitefly). The Tel Aviv population yielded a net reproductive rate of 34.6 times per generation under laboratory conditions, a value between the reproductive rates reported by Leddy et al. (1995) at 25 °C (49 times per generation) and 30 °C (8 times per generation) (Table 3). The lower reproductive rate in the California study at 30 °C resulted from the combination of lower fertility and lower preimaginal survival than exhibited by the Tel Aviv population. Overall, this comparison indicates that the differences in the demography of the two populations were minor.

The population of *E. inaron* in California originated from collections in Tel Aviv. Nonetheless there were differences in biology between the results obtained in this study vs. those of a laboratory study in California (Gould et al., 1995). Individuals in the latter study had a statistically insignificant, shorter developmental time at 30 °C than obtained in the present study. This faster development may reflect the different developmental rates of the host whitefly on the different host plants used in the two studies (*P. granatum* in Tel Aviv and *F. uhdei* in California). However, in both Tel Aviv and California synchrony between the parasitoid and whitefly host permits coincident development; thus lack of developmental synchrony should not be a factor limiting interactions between the host and parasitoid. The sex ratio of *E. inaron* from the California laboratory study was 74% female, while the sex ratio reared from field-collected individuals in Tel Aviv was 52% female. These differences probably represent different allocations of sex to offspring in the different experimental conditions.

We next extended the study to examine the quantitative impact of the parasitoid on the mortality of the whitefly in the field in Israel. The greatest mortality factor acting on the Tel Aviv population was the unassigned mortality that occurred in all stages (being greatest in the egg-to-second nymphal instar). It was also a significant component appearing in field life tables of *S. phillyreae* in California (Gould et al., 1992), where unassigned mortality was significantly greater in plots where parasitism was greater, indicating a possible relationship to parasitoid activities such as host feeding (Gould et al., 1992). The predominance of unassigned mortality was also demonstrated in population studies of the whitefly *Bemisia tabaci* (Gennadius) in Israel (e.g., Horowitz et al., 1984). In the present study, unassigned mortality generally increased throughout the season, while the presence of predators decreased, and the rates of parasitism first increased and then decreased; thus, unassigned mortality was related to neither the rate of parasitism per leaf nor to the presence of predators. It is possible that, in Tel Aviv, the unassigned mortality reflected the failure of first instar nymphs to establish themselves at suitable feeding sites on leaves, and that this establishment became more difficult as the season progressed and the leaves matured.

Life-table analyses indicate that parasitism played an important role in this system in both California and Tel Aviv. However, the impact of *E. inaron* was much greater in the California study, where its presence reduced the net growth rate of the population from 5 to 9 times per generation to near or below unity (Gould et al., 1992). In Tel Aviv the parasitoid was responsible for less overall mortality. Life tables showed variable whitefly reproductive rates: greater than unity early in the season, closer to unity in July when parasitism reached its greatest values, and below unity in September–October, when parasitism was low.

The present study identified density-dependent relationships between the presence of the parasitoids or predators and the density of hosts. Such a relationship may have arisen directly from density dependent discovery of host-bearing leaves; or from random examination and discovery of leaves combined with longer searching times on leaves bearing more hosts; or from both of these acting together. We know of no olfactory attraction to infested leaves by *E. inaron* (Bellows, unpublished), but the presence of honeydew is known to cause arrestment and leads to longer searching times in some other whitefly parasitoids (Shimron et al., 1992). Overall, this comparison of the two systems indicates that the populations were indeed biologically similar. However, there were important differences in role and impact that the natural enemies played in the separate systems.

We now turn to the question of whether our quantitative study of the *S. phillyreae*–*E. inaron* system in its area of origin could indicate the parasitoid's potential in a new environment. First, we note that *E. inaron* was the most common parasitoid recovered from the whitefly where it was collected in Tel Aviv [although there are several parasitoid species known from this whitefly (Bellows et al., 1990)]. Second, we consider the rate of parasitism attributable to this parasitoid. In periods when parasitoids were most abundant and parasitism was greatest, real (generational) mortality assignable to the parasitoid in Israel was 14%, and the marginal (stage-specific) rate for parasitoid-caused mortality in the fourth instar was 77.5%. For most of the season, however, parasitism rates were much lower (24–34%), generational mortality assignable to *E. inaron* was less than 10%, and the unassigned mortality did not appear to be related to presence or action of the parasitoid. Population growth rates in the field, even in the presence of the parasitoid, were generally greater than unity, and when the rates were lower than unity, parasitism was only moderate (and hence less of a contributing factor). Finally, we note a moderate density dependence in the likelihood of a parasitoid being reared from a leaf, but no density dependence in parasitism rates on individual leaves. Thus there was only limited (but positive) indication of a density-dependent numerical response on the scale of measurement used in this study.

In comparison to these findings, life table studies in California showed real mortality from parasitism ranging from 5 to 17%, with marginal rates of parasitism of up to 88% with additional mortality attributable to host feeding by the parasitoid (Gould et al., 1992). The parasitoid's impact as seen in the life tables was profoundly more significant in California. A net population growth rate of 5–9 times per generation in the absence of the parasitoid was reduced to near or below unity in the presence of the parasitoid thus limiting the growth rate of the whitefly population to stable numbers. In neither Tel Aviv nor California would measurements of generational mortality or of stage-specific mortality have unambiguously indicated the potential significance of the parasitoid. Even the complete life table studies in Tel Aviv failed to predict the important role in limiting population growth rates in California, indicating rather that the parasitoid was only partly effective at reducing population growth, and only for part of the season.

Several authors have suggested that the ecological and biological characteristics of natural enemies could be useful in predicting their value in a biological control system (see DeBach and Rosen, 1991; Ehler, 1990; Stilling, 1993; Waage, 1990, for discussions). These traits include high rate of increase, host specificity, high searching rate or efficiency, synchronized parasitoid–host life histories, and density-dependent response (Huffaker et al., 1977). Other ideas, such as obtaining the natural enemy stock from low host populations in the field, are derived from biological or ecological theory (Waage, 1990).

Our results shed additional light on the usefulness of some of these traits. First, we note that although the exact host range of *E. inaron* is not known, it is not host specific. It was reared extensively from *B. tabaci* whenever its culture sites were adjacent to the experimental sites at Tel Aviv University (Gerling, personal observations). Moreover, it is also known in Israel from *Aleyrodes singularis* Danzig, which develops in a very different habitat (Guershon and Gerling, 1994; Polaszek et al., 1992). However, the latter record must be re-examined in light of the recent molecular study of *E. inaron* and its related species, *E. estrellae* (Manzari et al., 2002). Its extraordinary effectiveness on one host (*S. phillyreae*) thus corresponds with the suggestions of Gerling (1992) that, in whiteflies, host specificity and long-term co-evolved relationships may not be essential attributes of effective natural enemies. Second, our results provide some quantification to the importance of “high search efficiency” e.g., Huffaker et al. (1977). *E. inaron* was reared from 23.8% of the studied leaves (66 of 277). The ratio of parasitoids to third instar nymphs on those leaves with *E. inaron* was 47.2%, and the ratio of parasitoids to third instar nymphs on all leaves was 24.6%. High search efficiency resulting in parasitism levels that bring about control is usually associated with values that

are closer to 100%. Yet, the observed “moderate” values were clearly associated with a parasitoid that was proven a successful natural enemy. Third, the *E. inaron* originally collected and sent to California was from heavily infested *P. granatum* leaves, i.e., from high, albeit local, and host densities. Our later studies have shown that it was an efficient parasitoid at both low densities (in both Israel and California) and high densities (in California, Bellows et al., 1992). Finally, our studies elucidate the comparative value of net reproductive rate as an indicator of natural enemy potential. We note that the increased growth rate of *E. inaron* under laboratory conditions with unlimited host supply was 69.3 (Gould et al., 1995). Future studies should quantify this variable for other natural enemies to determine its potential usefulness in other systems.

Overall, we measured few attributes in the native location for *E. inaron* that could be related to its performance in California; but none were unequivocally indicative of its proven potential. Yet, we have reaffirmed a number of valuable parameters in selection of the appropriate parasitoid. These include the premise that climatic similarity and correct host insect identity need to be considered. Moreover, the faster generation time of the parasitoid than its host and the fact that *E. inaron* was the principal parasitoid of *S. phillyreae* at both low and high local population levels where it was collected, also suggest its suitability.

One lesson to be learned from our inability to add guidelines for the a priori selection of natural enemies through studies of a natural enemy in its native environment, relates to the inherent differences in the nature of the two locations. Well-acknowledged differences that are innate to different natural habitats, no matter how climatically similar they may be, include those in the native flora and fauna. In the native habitat, the tested parasitoid often has difficulties finding its host and may compete for it with native natural enemies. In the introduced situation the natural enemy often, initially, faces an abundant host supply and little or no competition, i.e., conditions that are qualitatively very different to its native system. Later, density reduction and possible stability of the pest and natural enemy populations may follow. This new situation often includes newly established host insect levels and native competitors that did not exist before. We cannot anticipate which, if any, of these differences will be significant. Moreover, in most cases it is impractical to study them in their new location because they will not be duplicable in the native home. Therefore, we concur in general with DeBach and Rosen (1991) that “the ultimate success of a given natural enemy candidate for importation cannot be accurately predicted in advance.” However, our studies have also shown that investigating the attributes of successful natural enemies may nonetheless, equip the explorer with a more refined tool for his search.

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