Oviposition, Development, and Survivorship of *Encarsia pergandiella* (Hymenoptera: Aphelinidae) in Four Instars of *Bemisia argentifolii* (Homoptera: Aleyrodidae)

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ABSTRACT Oviposition, development, and mortality of *Encarsia pergandiella* Howard in the 4 instars of *Bemisia argentifolii* Bellows & Perring were evaluated under choice and no-choice conditions in the laboratory. *E. pergandiella* oviposited in all nymphal stages of *B. argentifolii*, but preferred 3rd and 4th instars. Regardless of host stage parasitized, adult wasps emerged from host pupae. The costs of oviposition in younger instars were delayed development, presumably to allow for growth and maturation of the host, and increased mortality of both parasitoid and host. Our results indicate that *E. pergandiella* can successfully exploit whitefly populations of both high and low densities by favoring large hosts of high quality when abundant, but shifting to, and successfully exploiting younger instar hosts of lower quality when necessary.

KEY WORDS sweetpotato whitefly, parasitoids, biological control, oviposition preference, parasitoid development

Bemisia argentifolii BELLOWS & Perring, is one of the most important pest insects of vegetables, broadleaf field crops, and ornamentals in the southern United States. The rapid rise of *B. argentifolii* to key pest status has been attributed, in part, to insecticide resistance and decimation of natural enemies in response to broad spectrum insecticides (Prabhaker et al. 1985, 1992). Therefore, biological control could be an attractive management alternative for *B. argentifolii* (Stansly et al. 1994).

A rich complex of at least 11 species of parasitoids of *B. argentifolii* in the genera *Encarsia* and *Eretmocerus* have been identified from Florida and the Caribbean (Evans 1993, Hoelmer et al. 1994). *E. pergandiella*, the most abundant in southern Florida, is a solitary autoparasitoid: females lay fertilized eggs in whitefly nymphs that develop into females, thereby functioning as primary parasitoids, but lay unfertilized eggs that develop into males in female pupae of primary whitefly parasitoids including conspecifics. The biology of *E. pergandiella* parasitizing greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood) was studied on field crops in California (Gerling 1966); reproductive strategy on the same host was studied by Hunter (1987, 1989). However, the biology of this parasitoid in respect to nymphal stages of *B. argentifolii* is not well documented. We report on oviposition, development time, and survivorship of *E. pergandiella* on different nymphal stages of *B. argentifolii*.

Materials and Methods

Parasitoids, Hosts, and Plants. *E. pergandiella* used in this study was originally collected on tomato in southwest Florida and identified by G. A. Evans (University of Florida, Gainesville). *B. argentifolii* was obtained from D. J. Schuster (Bradenton, FL) in 1990 and identified by T. M. Perring (University of California, Riverside). Voucher specimens of *E. pergandiella* and *B. argentifolii* have been deposited in the Insect Collection, Southwest Florida Research and Education Center, University of Florida, Immokalee, FL.

Whiteflies and parasitoids were maintained in an air-conditioned greenhouse on potted tomato, *Lycopersicon esculentum* Miller, 'Lanai' (1 plant per 15-cm pot), sweet potato, *Ipomoea batatas* L., collard, *Brassica oleracea* L. variety *acephala*, 'Georgia LS', and hibiscus, *Hibiscus rosa-sinensis* L. Plants were grown in Metro-Mix 300 growing medium (Grace Sierra, Horticultural, Milpitas, CA), and were fertilized with a slow release fertilizer (N:P:K, 12:8:6) (Diamond R Fertilizer, Winter Garden, FL).

Sweet potato leaves individually rooted in media cubes (Oasis, Smither-Oasis, Kent, OH) were used to maintain immature *B. argentifolii* nymphs exposed to *E. pergandiella* experimentally as described (Liu and Stansly 1995). Rooted leaves were held in 2 types of cages: wood frames (60 by 60 by 80 cm) with openings (5 or 10 cm in diameter) on sides and top covered with 52-mesh polyethylene screen (Lumite 25, Chiopee, Gainesville, GA);

and 0.9-liter clear, plastic cups, each with a 9-cm opening on top screen with nylon organdy and a corked access hole (1.2 cm in diameter) on the side. All experiments were conducted in an air-conditioned insectary at 26.7 ± 2°C , 55 ± 5% RH. Photoperiod was set at 14:10 (L:D) h with light intensities measured as photosynthetically active radiation at 39–44 μmol m^{-2} s^{-1} inside cages (LI-COR, Steady State Porometer, Model LI-1600, Lincoln, NE).

Parasitization and Oviposition Preference. *No-Choice.* Only 1 whitefly instar was exposed to parasitoids at a time. Forty unsexed whitefly adults were introduced onto a rooted sweetpotato leaf inside a cup-cage for a 4- to 5-h oviposition period to assure stage uniformity. When nymphs had developed to the desired stage (1st, 2nd, 3rd, or 4th instar), 5 female parasitoids were introduced into each cage for a 48-h oviposition period. Following a 2-wk incubation period, whiteflies were examined under a binocular stereoscopic microscope to determine number parasitized, living and unparasitized, dead, or emerged. Each experiment for each whitefly instar was replicated 8 times and was repeated 3 times.

Two-Instar Choice. Five combinations of paired whitefly instars were tested: 1st versus 2nd, 1st versus 3rd, 2nd versus 3rd, 2nd versus 4th, and 3rd versus 4th. Both nymphal instars were provided on the same leaf by collecting whitefly eggs inside a leaf clip-on cage at a different time at 3- to 9-d intervals. The location of each instar on the leaf was alternated to either the right or left side of the leaf to eliminate bias (Fig. 1). Two leaves were used as no-choice controls, one leaf with the younger, and the other with the older instars. We tried to collect the same number of whiteflies of each instar to avoid any bias resulting from host abundance. When whiteflies reached the desired stadia, 5 parasitoid females were introduced into the cup-cage for a 48-h oviposition period. Each treatment was replicated 8 times and the experiment was repeated 3 times.

Multiple-Instar Choice: Same Leaf. All 4 whitefly instars were offered simultaneously to parasitoid adults on the same leaf. The arrangement was made by collecting whitefly eggs for 4–5 h in cup cages containing 50 unsexed whitefly adults on the same sweet potato leaf at 3-d intervals. Leaves were examined daily and newly settled whiteflies circled with ink of a color specific to each oviposition interval, later corresponding to nymphal stage exposed to parasitoids. Similar numbers of whiteflies of each instar were collected to avoid any bias resulting from host abundance. After completion of the oviposition and incubation cycle, 10 parasitoid females and 2–3 males were introduced for 48 h into a cup cage containing the infested leaf. Parasitized, unparasitized, dead, and emerged whiteflies were recorded 2 wk later. Each treatment was replicated 8 times and the experiment was repeated 3 times.

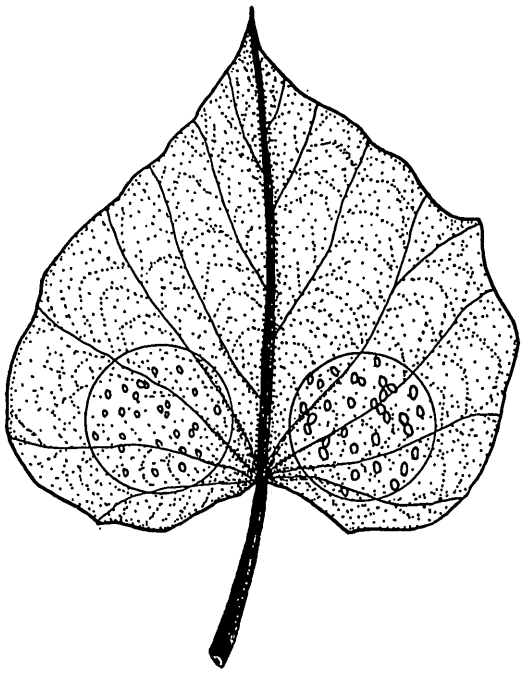

Fig. 1. Collection scheme for 2 different instar cohorts of *B. argentifolii* nymphs on rooted sweet potato leaves using clip cages.

Multiple-Instar Choice: Separate Leaves. Five rooted sweet potato leaves, each bearing approximately equal number of 1 developmental stage (egg, 1st, 2nd, 3rd, and 4th instars) of *B. argentifolii* were arranged in a 15-cm circle inside a wooden frame cage. A glass eye-dropper (0.5 by 5 cm) into which 25 parasitoid females had been aspirated was placed upright in the center of the circle to allow wasps to escape and gain access to the whitefly bearing leaves for 48 h. Leaves were then removed and incubated individually in cup-cages for 2 wk, and examined as above. Each treatment was replicated 8 times and the experiment was repeated 3 times.

Development. Whitefly eggs were collected and monitored on rooted sweet potato leaves as described above until the appropriate nymphal stages were attained. Five parasitoid females were allowed access to nymphs in a cup cage for 24 h. Nymphs were examined daily beginning the 7th d after exposure to parasitoids, and those with displaced mycetomes or visible parasitoid larvae were marked by circling with a ball point pen. Thereafter, parasitized nymphs were observed daily until all parasitoids had emerged or died. A total of 66 female parasitoid pupae was initiated in 1st instars, 53 in 2nd instars, 108 in 3rd instars, and 113 in 4th instars. Parasitoids that did not emerge from these marked whiteflies were considered dead, as were apparently unparasitized whiteflies that did not emerge.

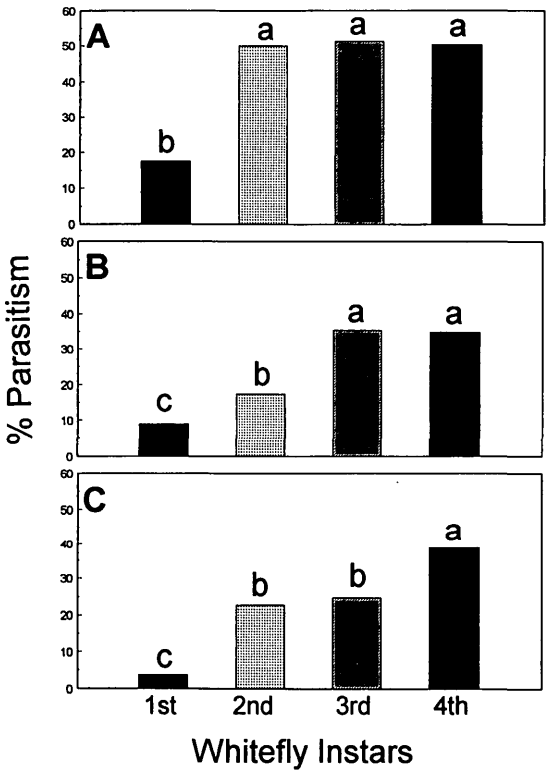

Fig. 2. Parasitization of *B. argentifolii* nymphs by *E. pergandiella*. A, no-choice test (a single whitefly instar exposed to parasitoids [$F = 4.9$; df = 3, 20; $P = 0.011$]); B, multiple-choice test, all 4 whitefly instars exposed to parasitoids on 4 different leaves ($F = 19.5$; df = 3, 77; $P = 0.0001$), and C, multiple-choice test, all 4 whitefly instars on the same leaf ($F = 23.4$; df = 3, 55; $P = 0.0001$). Bars in each figure with the same letter on top represent mean percents that do not differ significantly ($P < 0.05$, LSD [SAS Institute 1988]).

For development of males, female parasitoid pupae ≈24 h old were obtained from 3rd and 4th-instar whiteflies on rooted sweet potato leaves. The pupae were exposed to unmated parasitoid females <48 h old in a cup cage for 24 h. Parasitized female pupae ($n = 62$) in which the male larva was recognizable were marked using an ink pen 4–5 d after exposure. These parasitized pupae were observed daily thereafter until all live parasitoids had emerged.

Data Analysis. Mean percentage of parasitism and mortality was transformed to the arcsine square root [arcsine (percent mortality/100)$^{1/2}$] to stabilize error variances (Gomez and Gomez 1984), before being subjected to analysis of variance (ANOVA, SAS Institute 1988). Although there were no significant effects among the 3 repetitions in each experiment after a 2-way ANOVA, repetitions were pooled giving $n = 24$ replicates for each experiment. Means were separated using the least significant difference (LSD) test following a significant F test, and untransformed means were reported.

Table 1. Mortality of immature *E. pergandiella* and of unparasitized *B. argentifolii* on sweet potato leaves after individual instars were exposed to 5 *E. pergandiella* females in no-choice tests for 48 h in a cup-cage (24 replicates)

Whitefly instar	Whiteflies, n	% mortality ± SE	
		Parasitoids	Whiteflies
1st	259	13.5 ± 2.4a	42.7 ± 7.5a
2nd	513	12.5 ± 2.1ab	13.1 ± 2.3b
3rd	432	11.8 ± 2.1ab	11.4 ± 5.4b
Early 4th	331	10.6 ± 2.0b	17.2 ± 5.0b
F		6.12	5.31
P		0.04	0.007

Mean percentages in the same column followed by the same letters do not differ significantly ($P < 0.05$, LSD [SAS Institute 1988]).

Results

Parasitization and Oviposition Preference. *E. pergandiella* oviposited in all 4 instars of *B. argentifolii*, although there were differences among hosts in oviposition rate, preference, and subsequent development time of the parasitoid. Adults emerged from whitefly 4th instars or "pupae" regardless of host stage at oviposition.

No-Choice. Significant differences in parasitization among whitefly instars were caused primarily by less parasitization of 1st instars compared with older instars (Fig. 2A). Greatest apparent mortality of parasitoids was observed in 1st instar hosts (Table 1). Mortality of exposed 1st instars not producing parasitoids was >3 times greater than of other host stages (Table 1).

Two-Instar Choice. Parasitization rate of early instars was always lower than that of older instar hosts (1st versus 2nd, 1st versus 3rd, 2nd versus 3rd, and 2nd versus 4th instar, Fig. 3). Similar results were obtained from no-choice controls except that differences were generally less pronounced and there were no significant difference between 2nd and 3rd instars. Mortality of unparasitized whiteflies in all 2-instar choice tests was not significantly different between the 2 instars except for instars 1 and 2. In this case, mortality of 1st instars was greater than of 2nd instars (Table 2).

Multiple-Instar Choice: Same Leaf. Differences in parasitism rate among instars were even more pronounced when all instars were available on the same leaf. 3rd and 4th instar hosts were preferred to 2nd instars, which were preferred in turn to 1st instars (Fig. 2B). Apparent mortality of parasitoid immatures did not differ significantly among host instars when choices were provided, although there was greater mortality of 1st and 2nd instar hosts than of 3rd or early 4th instars (Table 3).

Multiple-Instar Choice: Separate Leaves. Differences in parasitization among host instars were again pronounced, although in this instance 4th in-

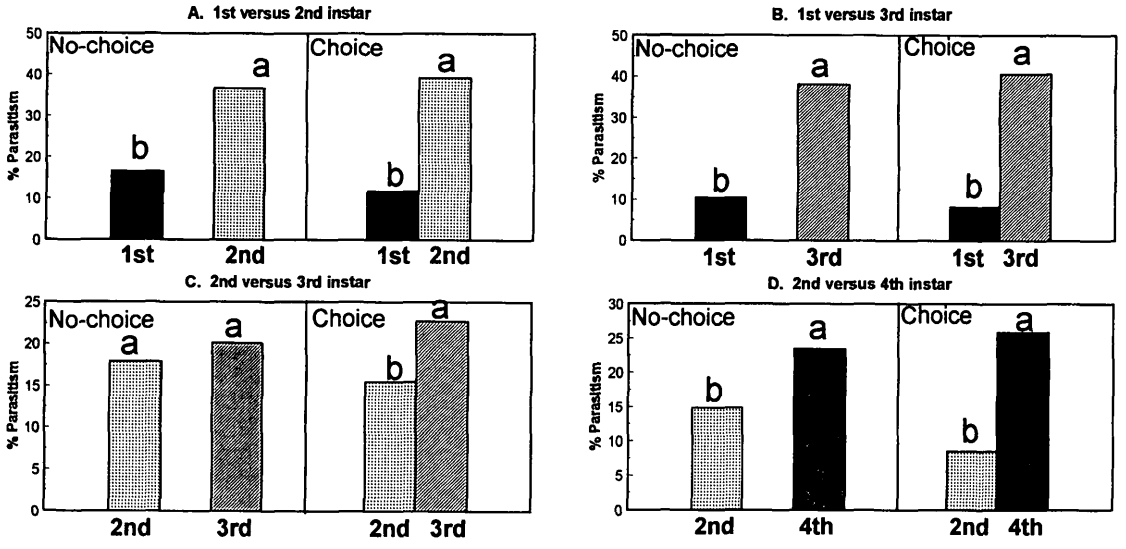

Fig. 3. Parasitization of 2 instars of *B. argentifolii* by *E. pergandiella* with and without choice: (F = 87.2; df = 1, 79; P = 0.001 for 1st versus 2nd instar; F = 105.5; df = 1, 75; P = 0.001 for 1st versus 3rd instar; F = 5.3; df = 1, 95; P = 0.024 for 2nd versus 3rd instar; F = 8.3; df = 1, 47; P = 0.007 for 2nd versus early 4th instar). Paired bars with the same letter on top represent mean percentages that are not significantly different (P < 0.05, LSD [SAS Institute 1988]).

stars were preferred to all other host stages; the parasitism rate of 2nd and 3rd instars was statistically indistinguishable (Fig. 2C). As when all instars were offered on the same leaf, apparent mortality of parasitoid immatures was not significantly different among host instars (Table 4). Mortality of unparasitized whiteflies exposed to parasitoids was also not significantly different among whitefly instars, although the data was suggestive of greater mortality of 1st instars than 4th instars.

Table 2. Mortality of *B. argentfolii* on sweet potato leaves after 2 instars on the same leaf were exposed to *E. pergandiella* adults with a single instar on 2 separate leaves as control

Paired-instar choice	Whiteflies, n	% mortality ± SE	
		Younger	Older
1st vs 2nd instar			
1st vs 2nd	3,685	30.0 ± 2.5	18.0 ± 1.2*
Single instar	2,833	34.7 ± 2.3	19.9 ± 1.3*
1st vs 3rd instar instar			
1st vs 3rd	3,295	16.4 ± 1.7	16.4 ± 1.4
Single instar	3,720	17.3 ± 1.4	16.0 ± 1.7
2nd vs 3rd instar			
2nd vs 3rd	3,294	17.4 ± 1.5	17.0 ± 1.5
Single instar	3,720	18.9 ± 1.5	18.1 ± 1.6
2nd vs early 4th instar			
2nd vs early 4th	2,272	10.4 ± 1.7	8.8 ± 1.0
Single instar	2,834	10.0 ± 1.7	8.7 ± 1.1

Mean percentages in the same row followed by an * differ significantly (P = 0.05, LSD [SAS Institute 1988]).

Development. *E. pergandiella* females developed successfully from egg to adult when initiated in all 4 instars of their whitefly hosts, albeit not at the same rate (Table 5). The earlier the instar parasitized, the more time was required to complete development, ≈50% more for 1st instars than for 4th instars. The delay for corresponded approximately to the time required for the whitefly host to develop to 3rd instar. Development rate of male parasitoids was like that of females initiated in 3rd-instar hosts: 9.14 d (SE = 0.14 d) for egg and larval stages and 3.90 d (SE = 0.11 d) for the pupal stage, for a total of 13.04 d (SE = 0.15 d) from egg to adult (n = 77). There were no significant effects of host stage on survivorship of parasitoids during the late larval–pupal stage. Emergence was

Table 3. Mortality of immature *E. pergandiella* and of unparasitized *B. argentifolii* on sweet potato leaves when all 4 instars on the same leaf were exposed to 5 *E. pergandiella* females for 48 h in a cup-cage (24 replicates)

Whitefly instar	Whiteflies, n	% mortality ± SE	
		Parasitoids	Whiteflies
1st	506	9.6 ± 1.3	28.2 ± 3.2a
2nd	571	6.7 ± 1.9	24.7 ± 2.0a
3rd	551	8.6 ± 2.4	15.4 ± 1.4b
Early 4th	632	8.2 ± 1.3	14.4 ± 1.8b
F		0.22	4.04
P		0.09	0.01

Mean percentages in the same column followed by the same letter do not differ significantly (P < 0.05, LSD [SAS Institute 1988]).

Table 4. Mortality of immature *E. pergandiella* and of unparasitized *B. argentifolii* on sweet potato leaves after all 4 instars on separate leaves were exposed to *E. pergandiella* females for 48 h in a wooden frame cage (16 replicates)

Whitefly instar	Whiteflies, *n*	% mortality ± SE	
		Parasitoids	Whiteflies
1st	1,555	8.2 ± 1.1	6.2 ± 1.3
2nd	1,429	7.6 ± 0.6	8.0 ± 1.2
3rd	1,529	9.2 ± 0.7	7.7 ± 0.9
Early 4th	1,760	9.7 ± 1.2	9.9 ± 1.0
F		1.65	2.53
P		0.08	0.07

Mean percentages in the same column followed by the same letters do not differ significantly ($P < 0.05$, LSD [SAS Institute 1988]).

89.6% over all host stages for females, and 83.9% for males.

Discussion

Parasitization and Oviposition Preference. We have used preference to refer to the propensity of *E. pergandiella* females to oviposit into late instars as indicated by resulting higher levels of parasitization. We admit the possibility that differential egg or early larval mortality would give a similar result, but think it unlikely, given that we have no independent evidence for such differential mortality. Also, Nechols and Tauber (1977) verified an ovipositional preference for 4th instar *T. vaporariorum* by *E. formosa* by dissecting out parasitoid eggs from the host nymphs. *E. pergandiella* females were able to parasitize all sessile developmental stages of *B. argentifolii*, but preferred 3rd and 4th instars. Using *T. vaporariorum* as the host, Gerling (1966) reported that this parasitoid oviposited in all stages but preferred 2nd and 3rd instars. Nell et al. (1976) and Nechols and Tauber (1977) observed that *E. formosa* preferred 3rd and 4th instars and prepupae of *T. vaporariorum* for oviposition, whereas Enkegaard (1993) reported that *E. formosa* preferred 4th and prepupal stages of *B. tabaci*. Our results support the conclusion that *E. pergandiella* prefers 3rd and 4th (including early pupal) instars of *B. argentifolii* for oviposition.

A preference for later instars is perhaps not surprising, because larger hosts provide immediate resources for larval development, thereby maximizing intrinsic rate of increase (r) through decreased generation time, increased fecundity, or both. Examples of similar preferences can be encountered in other host–parasitoid systems. The aphid parasitoid, *Aphidius sonchi* Marshall preferred larger apteriform nymphs of *Hyperomyzus lactucae* (L.) that produced larger and more fecund offspring than smaller, less preferred instars (Liu et al. 1984, Liu 1985). However, the endoparasitoid *Microcharops anticarsiae* Gupta showed no preference when 2 or 4 consecutive instars of velvetbean cateroillar, *Anticarsia gemmatalis* Hübner, were offered (Patel and Habib 1993), indicating that perhaps there was little advantage in choosing a host with more resources than could be profitably used.

Development. Gerling (1966) reported that development time of *E. pergandiella* did not vary with nymphal stage of *T. vaporariorum* used for oviposition and larval development. In contrast, we found that development time of *E. pergandiella* decreased as the age of the *B. argentifolii* host receiving the parasitoid egg increased. Nechols and Tauber (1977) reported that all larval development of *E. formosa* subsequent to 1st instar occurred in 4th instar *T. vaporariorum*, regardless of instar attacked. Our results with *E. pergandiella* are consistent with the hypothesis that hatching or early larval development, or both, of *E. pergandiella* deposited into 1st or 2nd instars was delayed until the host developed to 3rd instar. The hypothesis is further supported by the fact that evidence of parasitization (displaced mycetomes) was not observed until the 3rd stadium, regardless of the stage attacked. The lack of any difference in egg + larval development of parasitoids when oviposition occurred in 3rd and 4th instars indicated no significant delay in 3rd instars. Furthermore, we found no difference in development rate between parasitized and unparasitized whiteflies (T.X.L., unpublished data) in concert with results reported for *E. formosa* (Nechols and Tauber 1977, Enkegaard 1993). It appeared that parasitoid development was arrested and host development proceeded unabated in parasitized 1st- and 2nd-instar hosts.

Table 5. Development time and percentage of survivorship of *E. pergandiella* females in specific nymphal stage of *B. argentifolii* on sweet potato leaves

Whitefly instar	*n*	Female development (day ± SE)			Survivorship, %
		Egg and larval	Pupal	Total	
1st	66	13.14 ± 0.22a	4.05 ± 0.11a	17.19 ± 0.36a	87.9
2nd	54	10.48 ± 0.19a	3.84 ± 0.10a	14.31 ± 0.31b	90.6
3rd	108	9.44 ± 0.11b	3.50 ± 0.08b	12.94 ± 0.16c	88.9
Early 4th	113	8.43 ± 0.06b	3.29 ± 0.05b	11.63 ± 0.07d	91.2
F		19.22	16.43	130.30	
P		<0.01	<0.01	<0.01	

Mean days in the same column followed by the same letters do not differ significantly (LSD, SAS Institute 1988).

Parasitoid Mortality. Significant differences in late larval–pupal parasitoid mortality among host instars was only detected under no-choice conditions (Table 1). When female parasitoids were presented with a choice of instars for oviposition, greater avoidance of young instars was observed, with no differences in parasitoid mortality among host instars (Tables 2 and 3). An additional factor favoring reduced use of less preferred host stages was the lower parasitoid to host ratios of these latter experiments. It appeared that reduced pressure on young instars reduced parasitoid mortality.

Host Mortality. Mortality of apparently unparasitized whiteflies followed a similar, although more accentuated pattern. Highest mortality (42.7%, Table 1) occurred when 1st instars were exposed to parasitoids with no other options for either host feeding or oviposition. Mortality of 1st instars was less when ample hosts were available, especially older instars (Table 2). Mortality of unparasitized 1st and 2nd instars exceeded that of 3rd and 4th instars when all instars were available on the same leaf (Table 3) but not on different leaves, where the trend seemed to be reversed (Table 4). It appeared that parasitoids left leaves containing only 1st instars, leaving these nonpreferred hosts largely unaffected by either host feeding (the probable cause of most mortality among apparently unparasitized hosts, Arakawa 1982) or parasitization (Fig. 3C). However, young instar hosts were used when encountered on the same leaf as older instars, especially for host feeding. Thus, host feeding would account for higher mortality of young instars than of older instars present on the same leaf (Table 3). Nell et al. (1976) reported most frequent host feeding by *E. formosa* on 2nd-instar *T. vaporariorum*, and that host feeding was the primary cause of mortality of unparasitized hosts.

Encarsia pergandiella displayed behavioral and physiological plasticity that enabled it to exploit host resources optimally under a broad range of relative host densities. When ample supplies of 3rd and 4th instars were available, these preferred hosts were used for oviposition and younger instars for host feeding. However, young instars were readily parasitized when nothing else was available, although development was delayed to allow time for host growth to provide adequate resources for larval development. Autoparasitism would offer yet another option under conditions of high parasitoid to host ratios, allowing exploitation of hosts parasitized by competing individuals of the same or other species (Hunter 1989, 1993).

Fecundity, survivorship, and thus intrinsic rate of increase would be maximized at high host densities by the choice of optimal hosts for female development. Less suitable hosts would be used as the supply of optimal hosts was depleted, with a cost in terms of lower r caused by reduced development rate and possibly increased mortality. Autoparasitism would also increase as fewer and fewer unoccupied hosts were available, further decreasing r by increasing males at the expense of females. The resulting numerical response to host availability would function to stabilize the host–parasitoid system, dampening populations cycles and thus the probability of extinction (Hassell et al. 1983). Stability of the parasitoid population should be a desirable management attribute, especially where parasitoid populations cannot be maintained by inundative release. Under such conditions, *E. pergandiella* could be the ideal candidate for biological control of *B. argentifolii*.

Acknowledgments

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