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DOES AN AUTOPARASITOID DISRUPT HOST SUPPRESSION PROVIDED BY A PRIMARY PARASITOID?

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Abstract. Theory predicts that intraguild consumers such as predators or parasitoids may displace more specialized heterospecific competitors and thereby actually increase the population densities of a shared host or prey. We tested this idea with a native primary parasitoid, *Eretmocerus eremicus*, and an exotic autoparasitoid *Encarsia sophia*, both attacking the sweetpotato whitefly *Bemisia tabaci*. Autoparasitoids are intraguild consumers that attack and kill both the immature stages of hemipteran hosts, such as whiteflies, and heterospecific and conspecific parasitoids.

In population cages on cotton plants in the field in 1997 and 1998, we introduced whiteflies and then parasitoids in a replacement design with constant total numbers of parasitoids, as follows: (1) control (whiteflies only), (2) *E. eremicus* only, (3) *E. sophia* only, and (4) both *E. eremicus* and *E. sophia*. Destructive samples of plants were taken 2, 4, and 6 wk after wasp releases, and immature whitefly and wasp stages were censused. In 1997, there were no significant differences in whitefly densities among treatments. In 1998, the control treatment densities were significantly greater than parasitoid treatments, but there was no difference among the parasitoid treatments, indicating equivalent suppression of whitefly populations by the two parasitoid species. In both years, similar patterns in parasitoid dynamics were observed. Densities of *E. eremicus* were significantly higher in the absence of *E. sophia*. In contrast, *E. sophia* densities were unaffected by the presence of *E. eremicus*. The results suggest that interference by the autoparasitoid reduced primary parasitoid density, but with no concommitant disruption of host suppression. The results support theoretical predictions that no disruption should occur when both parasitoids are equally efficient and suggest that an autoparasitoid may be as efficient as a primary parasitoid in suppressing host densities.

Key words: Bemisia argentifolii; Bemisia tabaci; *biological control;* Encarsia sophia; Eretmocerus eremicus; *exotic species; heteronomous hyperparasitoid; interference competition; interspecific competition; intraguild predation; population regulation; sweetpotato whitefly.*

INTRODUCTION

In recent years, the study of predator–prey population dynamics has expanded from the investigation of pairwise interactions of predators and their prey to investigations of interactions on both multiple and higher trophic levels (Polis and Myers 1989, Morin and Lawler 1995, Rosenheim 1998). Three types of interactions among predators may influence prey dynamics. In one type, secondary predator species that attack primary predators may cause trophic cascades that raise prey densities and/or change prey community structure (Fagan and Hurd 1994, McPeek 1998, Moran and Hurd 1998). A second type of interaction includes intraguild predators, predators that attack both a competitor (intraguild prey) and a common prey species. Intraguild predators are predicted to be superior competitors and may disrupt prey suppression when they are less efficient than the primary predator (Polis and Holt 1992, Rosenheim et al. 1993, 1995, Holt and Polis 1997). Lastly, predator species on the same trophic level may be nonadditive in their influence on common prey. They may act synergistically to enhance pest population suppression (Losey and Denno 1998) or antagonistically to reduce population suppression (Briggs 1993, Crowder et al. 1997). A common result of theoretical investigations of all of these three interactions is that the particular outcome is contingent on the life history and behavior of the interacting species.

Understanding the effects of intraguild interactions is particularly important and contentious in the field of classical biological control, where exotic natural enemies are released against exotic pests, and effective prey or host suppression is paramount. If interactions among predators or parasitoids can reduce the chance of successful control, then one or a few carefully chosen species should be released, and species that might disrupt pest suppression should be withheld from biological control introductions. The prevailing wisdom, however, is that competitive displacement should lead to more effective, not reduced, control. Evidence for

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this idea comes from several classic case studies of biological control following competitive exclusion (DeBach and Sundby 1963, DeBach 1966, Luck and Podoler 1985, Rose and Rosen 1991–1992). In these examples, pest densities appeared lower after competitive displacement, not higher. Nevertheless, negative effects of competition might explain cases in which unsuccessful or partial control persists despite continued introductions, or cases in which later introductions fail to establish altogether (Ehler and Hall 1982; but see Keller 1984).

Predictions from ecological theory on this issue are mixed. However, recent theory highlights the role of direct, lethal interference competition among natural enemies (Briggs 1993, Rosenheim et al. 1995, Murdoch et al. 1998). In the simplest theoretical view of two-predator–prey interactions, predators interact only via exploitative competition. The predator species that is predicted to win in competition is the one that drives the prey to a level below which its competitor can persist (Murdoch et al. 1998). In this case, the implication for biological control is clearly favorable, as there is no danger of disrupting pest suppression by introducing multiple predator species. The situation changes, however, when one or more mechanisms of interference competition are included, for instance, intraguild predation (Rosenheim et al. 1995, Holt and Polis 1997), or among parasitoids, multiparasitism, facultative hyperparasitism (Briggs 1993), or autoparasitism (Mills and Gutierrez 1996, Briggs and Collier 2001), the last of which is particularly relevant here. Population dynamic models that include one of these mechanisms of interference competition predict that the interfering intraguild predator, ''multiparasitoid,'' facultative hyperparasitoid, or autoparasitoid may in some situations competitively displace a more effective enemy species and thereby drive up pest equilibrium densities, i.e., disrupt or weaken effective biological control. This theory remains largely untested, however, and so has not generally influenced biological control practice.

Interspecific interactions involving ''autoparasitoids'' are perhaps the acid test of this controversy. Autoparasitoids may be capable of strong interference competition and are in many ways analogous to intraguild predators (Polis and Holt 1992, Rosenheim et al. 1995). Autoparasitoid females develop as primary parasitoids of immature whiteflies or scale insects (the primary hosts). Males, on the other hand, develop as hyperparasitoids; their hosts (the secondary hosts) are the immature stages of female conspecific and heterospecific parasitoids (Walter 1983, Hunter and Woolley 2001). The attack on heterospecific competitors by autoparasitoid females represents a mechanism of interference similar to intraguild predation. Like intraguild predators, autoparasitoids consume and kill both their competitors and a shared host (Rosenheim et al. 1995). Autoparasitoids are also similar to intraguild predators in that they are predicted to have the potential to disrupt pest suppression (Mills and Gutierrez 1996, Briggs and Collier 2001). Autoparasitoids have been introduced several times for classical biological control of whiteflies and armored scale pests, but have been considered to be questionable choices for introduction by some authors (Rosen 1981, Mills and Gutierrez 1996). We investigate the possibility that an autoparasitoid may disrupt pest suppression.

Methods

Experimental system

We conducted an experimental investigation of the effect of introducing a primary parasitoid, an autoparasitoid, or both parasitoid species to experimental populations of the sweetpotato whitefly *Bemisia tabaci* (Gennadius)(Hemiptera: Aleyrodidae) in field cages. Under the null hypothesis of no disruption of whitefly suppression, we expected that when both parasitoids were present, whitefly densities would be intermediate between the densities observed in the single parasitoid treatments. On the other hand, disruption would be indicated if whitefly densities in the both parasitoid species treatment approached, equaled, or surpassed the whitefly densities in the treatment with the less suppressive parasitoid species alone. The null hypothesis that interspecific interference has no influence on parasitoid populations would be supported by observations of similar dynamics of parasitoids in pairwise comparisons of single species vs. both parasitoid species treatments. Evidence of interspecific interference between the parasitoids would appear as differences in population growth trajectories, or extinction of one of the parasitoid species in the both treatment replicates but no extinction in the replicates of the single species treatment.

The subjects of this study are two parasitoids that have recently become sympatric in the Imperial Valley of California. *Eretmocerus eremicus* Rose & Zolnerowich (Hymenoptera: Aphelinidae) is a primary parasitoid and is the dominant native parasitoid of sweetpotato whitefly *B. tabaci* in the southwestern United States (Rose and Zolnerowich 1997). The autoparasitoid, *Encarsia sophia* (=*E. transvena* (Timberlake)) (Hymenoptera: Aphelinidae) is exotic, and was released in California as part of the classical biological control program for the exotic biotype of *B. tabaci* (biotype B = *B. argentifolii* Bellows & Perring) in the southern United States and other parts of the world (DeBarro 1995, Gerling 1996). *Encarsia sophia* has recently become established in the field (Roltsch et al. 1998). *Encarsia sophia* use *E. eremicus* immatures as secondary hosts (Hunter and Kelly 1998); thus theory predicts that the former species could reduce suppression of *Bemisia tabaci* provided by the primary parasitoid *E. eremicus*.

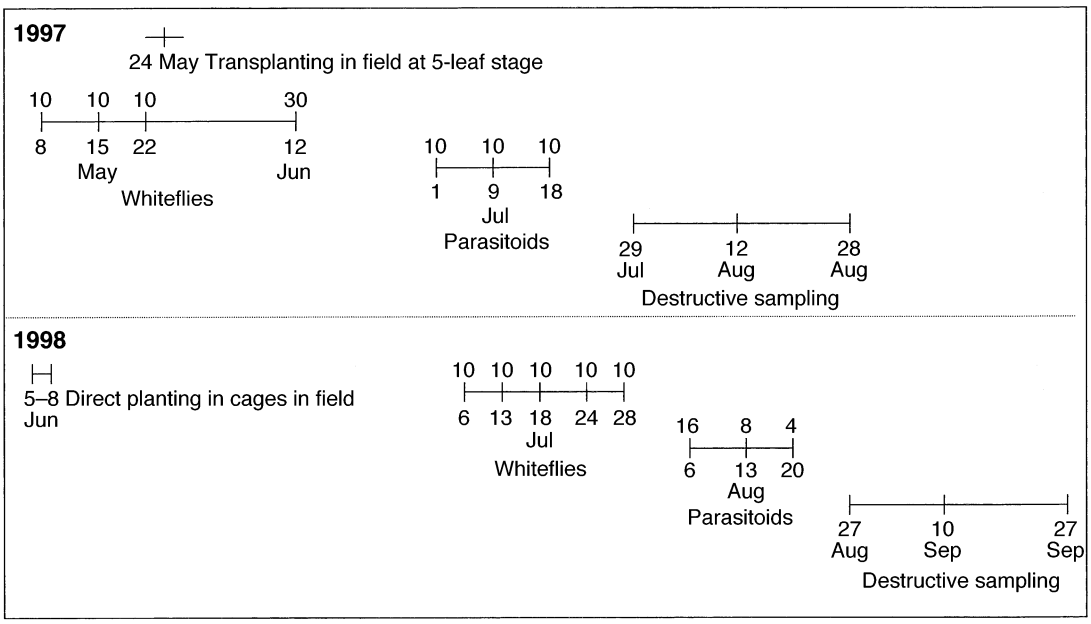

FIG. 1. Chronology of cotton planting, whitefly and parasitoid introductions, and field sampling in 1997 and 1998. Dates are below hatches. The numbers above the hatches represent the numbers of individuals introduced. For whiteflies, the numbers are the total number of males and females. For parasitoids, the numbers are the total number of females of one or both species. In all parasitoid introductions, at least one male of each species was introduced per cage. See *Methods*: *Field experiments* for details.

Insect cultures

Eretmocerus eremicus used in the experiments were purchased from a commercial insectary (Koppert Biological Systems, Incorporated, Romulus, Michigan) or were produced in our laboratory culture. Both sources originated from a population collected in a greenhouse in Phoenix, Arizona. The population of the autoparasitoid *Encarsia sophia* used in the experiments was originally collected in Murcia, Spain in 1993, and cultured at the USDA/APHIS Mission Biological Control Laboratory before being widely released in Texas, Arizona, and California. Both parasitoids were cultured on greenhouse whiteflies, *Trialeurodes vaporariorum* (Westwood) (Hemiptera: Aleyrodidae) on green beans *Phaseolus vulgaris* L. and were maintained in a walk-in environmental chamber at 27°C and on a 16L : 8D light: dark cycle.

Field experiments

Field experiments were carried out in 1997 and 1998. In each year, cotton plants were established in cages in an irrigated cotton field at the University of Arizona Campus Agricultural Center, Tucson, Arizona, USA, and *B. tabaci* adults and parasitoids of both species were introduced over periods of time according to treatment (see Fig. 1 for dates and numbers of individuals). Multiple introductions of both whiteflies and parasitoids were performed to reduce the variation in the availability of suitable whitefly and wasp host stages. Plants from each treatment were then sampled destructively on one of three sample dates and the leaves brought back to the laboratory for censusing. In the laboratory, whiteflies and wasps were censused, and the leaf area of all censused leaves was measured with a leaf-area meter (LI-COR, Incorporated, Lincoln, Nebraska). Details of the methods differed somewhat between years (Fig. 1, and see *Methods: 1997 season* and *Methods: 1998 season*).

In both years, field cages consisted of a large bag made of fine-mesh polyester silk screen (120 cm high and 55 cm diameter) with a drawstring bottom. Each cage was fixed to the top of the 3-gallon (11.4 L) pot containing the transplanted cotton plant in 1997, and in 1998 to a section of PVC drainage pipe (20 cm diameter), which was sunk into the soil around the cotton seedlings. In 1998, the cage was fixed to the pipe by a 9 mm wide plastic cable tie. Each cage was also attached to an exterior frame consisting of two intersecting inverted U-shaped rolled steel rods, spot welded at the intersection. The frame legs were sunk into the soil, and the frame anchored to the ground with nylon cord and tent pegs. The 1998 cage design prevented contamination from most insects, but did not prevent the entry of the omnivorous bug *Orius* sp. into some of the replicates. In analyses, however, the presence or absence of *Orius* did not significantly influence either whitefly density or the density of the two wasp species.

Wasps were introduced into cages in a replacement experimental design with four treatments: Control (no

wasps), ES (*E. sophia* only), EE (*E. eremicus* only), and Both (both species). On a given introduction date, half the number of female wasps of each species were introduced in the Both treatment. For instance, at the first wasp introduction in 1997, 10 female *E. sophia* were introduced to each ES cage, 10 female *E. eremicus* were introduced to each EE cage, and five females of each species were introduced to each Both cage. These ratios were used in all wasp introductions in both years. This experimental design is appropriate for determining the effect of interference competition on host or prey densities (Heinz and Nelson 1996). At each wasp introduction, at least one male of each species was included in each cage.

Censusing methods included subsampling when whitefly densities were high. All whitefly nymphs were counted on a leaf unless their number was estimated to be >100 nymphs. When nymph densities were estimated to be between 100 and 500 nymphs, portions of the leaf were censused between two major leaf veins (approximately one-half or one-fourth of the leaf depending on density) (Naranjo and Flint 1994). Several smaller circular areas (each 5.82 cm^2) were censused per leaf when estimated nymph densities per leaf exceeded 500 nymphs or when much of the leaf surface was obscured by mold growing on whitefly honeydew.

Immature parasitoids were censused as follows. Whitefly nymphs with displaced mycetomes (symbiont-housing organs) were counted as larval parasitoids. Second and third instar larvae of both wasp species cause displacement of these paired, yellow organs that can be seen through the translucent whitefly cuticle. We also distinguished and counted *E. eremicus* prepupae-pupae, *E. sophia* late larvae-prepupae, and *E. sophia* pupae. Previous work indicated that *E. eremicus* prepupae-pupae and *E. sophia* late larvae-prepupae are vulnerable to parasitism by *E. sophia*. The pupal stage of *E. sophia,* which is characterized by a melanized pupal sheath, is not preferred and is nearly invulnerable to parasitism (Hunter and Kelly 1998).

1997 season

In 1997, ~180 experimental cotton plants were grown in the greenhouse. *Bemisia tabaci* was introduced to plants three times starting when plants had their first true leaves, and the plants were then transplanted into cages in the field (Fig. 1). Observations of very few whitefly nymphs after transplantation prompted an additional introduction of 30 whiteflies per plant (Fig. 1). Three introductions of parasitoids were then made, followed by three destructive samples of plants, in which we sampled 9–11 plants per treatment. Infestation by secondary pests (cotton aphids and spider mites) interfered with whitefly reproduction on some plants. If, on a given sample date, a plant chosen to be sampled was badly contaminated, we chose a replacement or additional plant. Sampled plants were cut off at ground level and main stem leaves were removed and brought back into the laboratory for census under dissecting microscopes. All main stem leaves were censused unless there were 10 or more, in which case alternate leaves were censused. In 1997, censusing methods distinguished two classes of whitefly nymphs: red-eyed fourth instars and second through early-fourth instar nymphs. Nymphs in the latter class include the most vulnerable stages for wasp attack.

1998 season

In 1998, experimental cotton plants were planted directly into cages in the field in order to reduce infestation by secondary pests, and whitefly and parasitoid introductions were made later in the season (Fig. 1). Whiteflies were released when most plants had ~10 leaves. The actual numbers of wasps released per cage varied between introduction dates in 1998; this was due to variation in our supply of wasps in the laboratory (Fig. 1). In each sample, 15 replicates/treatment (60 plants total) were randomly selected and destructively sampled. In 1998, whole plants were brought back into the laboratory, all of the leaves were counted, and a large basal secondary stem was chosen for census. Secondary stems were chosen because leaves on the main stem tended to be old or had dropped. All leaves along the secondary stem were censused. Plants had approximately equal total numbers of leaves on all three sample dates (mean number ± SE; sample 1, 133.34 ± 5.86 leaves/plant, sample 2, 136.60 ± 5.48 leaves/plant, sample 3, 129.17 ± 5.45 leaves/plant). In censusing whitefly densities in 1998, we collapsed all whitefly stages into a single category ''whitefly nymphs,'' which included all instars including late fourth instar whiteflies. We collapsed age categories because we had observed that late stage fourth instar nymphs represented a small proportion of the whiteflies censused in 1997 and were not easily distinguished from slightly younger fourth instars.

E. sophia *parasitism rates*

In the 1997 field experiment, we compared the rate of parasitism of whitefly and wasp hosts by *E. sophia* in the ES and Both treatments. Samples of early fourth instar whitefly nymphs and wasp immatures were dissected in saline and examined for wasp eggs. *Encarsia sophia* lay female eggs inside the whitefly nymph. These eggs are easily distinguished from *E. eremicus* eggs, which are laid underneath the whitefly on the leaf surface. Male *E. sophia* eggs are laid on the outside of wasp larvae or pupae within the dry mummified remains of the whitefly. For each replicate of the ES treatment, 50 whitefly nymphs (selected from at least five leaves) and 50 *E. sophia* immatures were dissected. We preferentially dissected stages of *E. sophia* preferred for parasitism by conspecifics (late larval to prepupal stages) but also dissected the less preferred pupal stage to bring the total to 50. In the Both treatment,

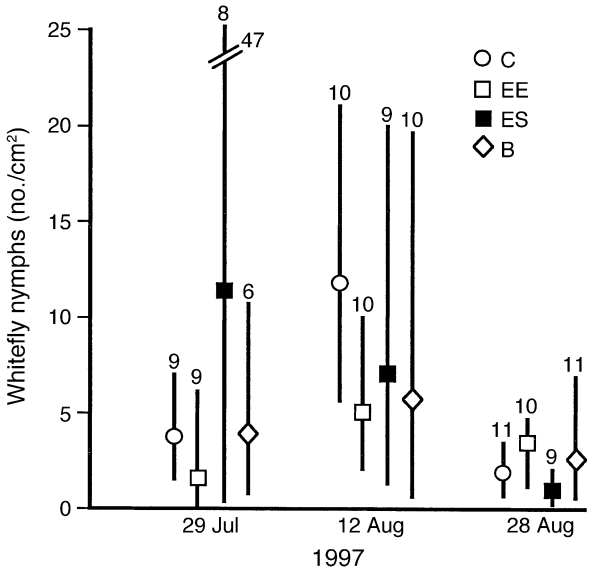

FIG. 2. Mean densities of whitefly nymphs in 1997. Key to abbreviations: C, no whitefly controls; EE, *Eretmocerus eremicus* (the primary parasitoid) alone; ES, *Encarsia sophia* (the autoparasitoid) alone; and B, both parasitoid species. Numbers above the bars are sample sizes. The means and 95% confidence intervals were back-transformed from cube-root estimates. The sample date was significant in its influence on whitefly density, but treatment was not (Table 1).

25 immature *E. sophia* and 25 *E. eremicus* were dissected per replicate.

Data analysis

Densities of whitefly nymphs, immature *E. eremicus*, immature *E. sophia* (combined late larval-prepupal stages and pupal stage), and total wasp densities were analyzed using ANOVA on cube-transformed data, with sample date and treatment as factors. Note that this experimental design does not call for a repeated-measures analysis because all replicates were sampled destructively and were thus independent. The cube root transformation was chosen over several other possible transformations as the one that minimized deviance, better equalized variances, and provided the best model fit to the data. In 1998, whitefly nymph density variances were not equivalent across different sample dates, so the three sample dates were analyzed separately, with only treatment as a factor.

The proportions of whitefly and wasp hosts containing *E. sophia* eggs were compared using the generalized linear modeling techniques available in the statistical package GLIM (McCullagh and Nelder 1983, Crawley 1993). GLIM performs a linear logistic analysis of deviance (equivalent to ANOVA for binomial data), and allows proportional data to be analyzed directly. Here the response variable was the number of hosts of a given type that contained *E. sophia* eggs and the binomial denominator was the number of hosts dissected of that type. The deviance among treatments is approximately χ^2-distributed for binomial data. In the first analysis, parasitism rates of the two secondary host types in the Both treatment were compared across all sample dates. In the second analysis, the response variable was the same but host type (primary or secondary), treatment (ES or Both), and sample date (1–3) were all included as factors. In all cases, Williams' correction was employed when greater than binomial variance was detected, leading to more conservative χ^2 estimates (Crawley 1993).

Primary *E. sophia* sex ratios were calculated by multiplying the proportion of a given host type that was parasitized by *E. sophia* by the density of that host type. The estimated sex ratio was then the mean density of hosts containing male eggs divided by the mean densities of all *E. sophia*-parasitized hosts.

RESULTS

1997 season

In 1997, whitefly densities were high and variable throughout the sampling period (Fig. 2). There was no statistically significant influence of treatment on whitefly densities; parasitoid treatments were not significantly different from the control treatment or from each other throughout the sampling period (Fig. 2, Table 1). Sample date was statistically significant, however and reflected a decline in whitefly densities across the three sample dates (Fig. 2, Table 1), probably due to plant senescence and the buildup of honeydew and mold on leaf surfaces associated with high whitefly densities. While parasitoids did not have a significant impact on whitefly densities in 1997, the effect of treatment on the two parasitoid densities differed. *E. eremicus* den-

TABLE 1. Analysis of whitefly densities, 1997 and 1998.

Source	df	*F*	*P*
1997			
Treatment	3	0.56	0.6427
Sample	2	4.38	0.0302
Treatment × Sample	6	1.47	0.3933
Error	96		
1998†			
Sample 1			
Treatment	3	0.67	0.5725
Error	54		
Sample 2			
Treatment	3	3.89	0.0260
Error	54		
Sample 2 wasp treatments only‡			
Treatment	2	0.03	0.9747
Error	41		
Sample 3			
Treatment	3	22.26	<0.0001
Error	49		
Sample 3 wasp treatments only‡			
Treatment	2	0.04	0.9573
Error	36		

† In 1998, densities were analyzed separately at each sample date because of unequal variances among sample dates.
‡ The control treatment was excluded from this analysis.

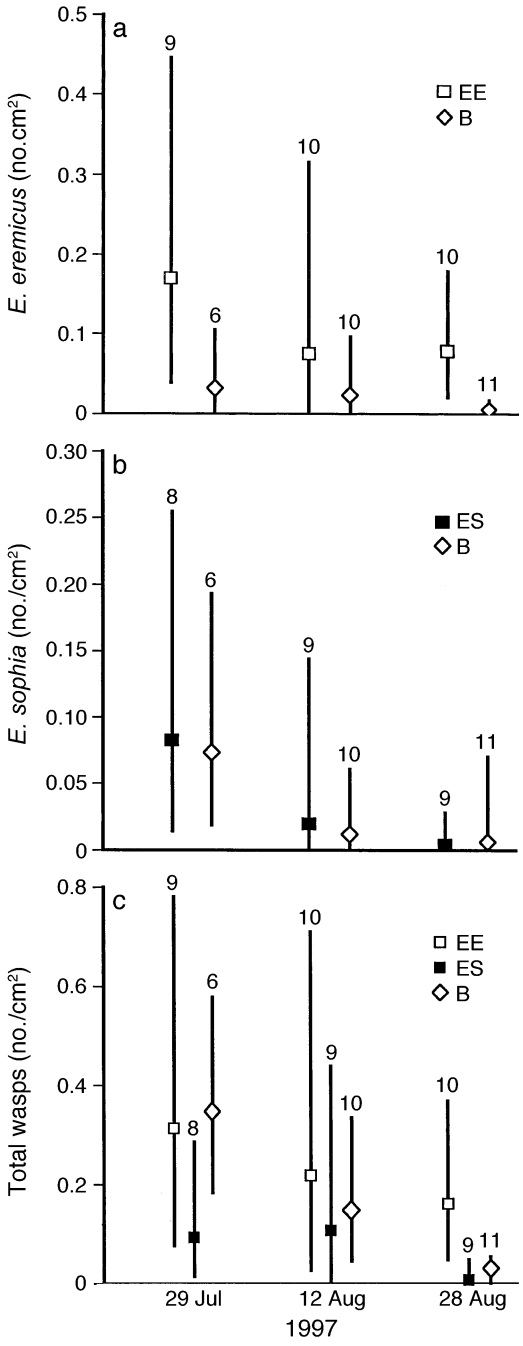

FIG. 3. Mean densities of wasp late-larval and pupal stages in 1997. The means and 95% confidence intervals were back-transformed from cube-root estimates. Key to abbreviations: EE, *Eretmocerus eremicus* (the primary parasitoid) alone; ES, *Encarsia sophia* (the autoparasitoid) alone; and B, both parasitoid species. Numbers above the bars are sample sizes. (a) The primary parasitoid, *E. eremicus*. The densities of *E. eremicus* were significantly higher in the EE-alone treatment than in the Both treatment (Table 2). (b) The autoparasitoid, *E. sophia*. The sample date had a significant influence on *E. sophia* densities, but treatment did not (Table 2). (c) Total wasps. Only the sample date was significant when the full data set was analyzed, but in an analysis of the last sample date, there were significantly higher densities of wasps in the EE-alone treatment than in the other two treatments (see Table 2 and *Results: 1997 season*).

sities were significantly lower in the Both treatment than in the EE alone treatment (Fig. 3a, Table 2), while treatment did not influence *E. sophia* densities (Fig. 3b, Table 2). Sample date had a significant influence only on the density of *E. sophia*, which declined throughout the sampling period following the decline in whitefly numbers (Fig. 3a). Although there was also an apparent decline in *E. eremicus* densities, it was not statistically significant (Table 2). A comparison of the total wasp densities in the three wasp treatments indicated a significant influence of sample date, and a marginal influence of treatment ($P = 0.08$; Table 2), probably due to differences at the third sample date (Fig. 3c). When the third sample date was analyzed separately, the total wasp density was significantly influenced by treatment ($N = 30$, $F_{2,27} = 3.93$, $P = 0.03$) due to the higher mean density of *E. eremicus* per square centimeter in the EE alone treatment (mean of 0.16 *E. eremicus*/cm², 95% CI: 0.05, 0.37) than *E. sophia* in the ES alone treatment (mean of 6.00×10^{-3} *E. sophia*/cm², 95% CI: 1.8×10^{-6}, 0.05) or both wasps combined in the Both treatment (mean of 0.04 wasps/cm², 95% CI: 1.4×10^{-3}, 0.06).

E. sophia *parasitism rates*

A greater proportion of *E. eremicus* immatures than *E. sophia* immatures were found to contain male *E.*

TABLE 2. Analysis of parasitoid densities.

Source	df	*F*	*P*
1997			
E. sophia			
Treatment	1	0.00	0.9757
Sample	2	4.00	0.0498
Treatment × Sample	2	0.08	0.9232
Error	47		
E. eremicus			
Treatment	1	10.62	0.0040
Sample	2	1.74	0.3720
Treatment × Sample	2	0.45	0.6402
Error	50		
Total wasps			
Treatment	2	3.43	0.0760
Sample	2	3.91	0.0493
Treatment × Sample	4	0.53	0.7140
Error	69		
1998			
E. sophia			
Treatment	1	0.10	0.7527
Sample	2	7.99	0.0014
Treatment × Sample	2	2.46	0.1843
Error	77		
E. eremicus			
Treatment	1	114.20	$\ll$0.0001
Sample	2	5.47	0.0119
Treatment × Sample	2	14.85	$<$0.0001
Error	80		
Total wasps			
Treatment	2	21.66	$<$0.0001
Sample	2	16.07	$<$0.0001
Treatment × Sample	4	4.60	0.0035
Error	119		

sophia eggs in the Both treatment, 0.15 vs. 0.06, but this difference was not statistically significant ($N = 40$, $\chi^2 = 1.87$, df = 1, $P = 0.17$). In the analysis of host selection across host types and treatments, the proportion of hosts with *E. sophia* eggs was not affected by any of the main effects; neither sample date (0.04 Sample 1, 0.04 Sample 2, 0.10 Sample 3, $\chi^2 = 4.32$, df = 2, $P = 0.12$, $N = 84$), host type (0.05 primary, 0.07 secondary; $\chi^2 = 0.12$, df = 1, $P = 0.73$, $N = 84$), nor treatment (0.06 ES alone, 0.06 Both; $N = 84$, $\chi^2 = 0.98$, df = 1, $P = 0.32$). The treatment-by-host type interaction was significant, however ($\chi^2 = 4.76$, df = 1, $P = 0.03$, $N = 84$); a greater proportion of primary hosts were attacked in the ES alone (0.08) than in the Both treatment (0.03), while more secondary hosts were parasitized in the Both treatment (0.09) than in the ES alone treatment (0.04).

The similar rates of parasitism of the two host types translated into extremely female-biased sex ratios because of the difference in the densities of the primary and secondary host types. Across all sample dates and both ES alone and Both treatments, the density of female *E. sophia* eggs in primary hosts was 0.35 ± 0.17 eggs/cm^2, mean ± 1 SE, while the density of male *E. sophia* eggs in secondary hosts was 0.008 ± 0.004 eggs/cm^2, yielding a primary sex ratio estimate of 2 % males.

1998 season

In 1998, whitefly densities were much lower overall but increased in the control treatment throughout the season (Fig. 4). Treatment had a significant influence on whitefly densities on the second and third sample dates (Fig. 4, Table 1). On the third sample date, the effect of treatment was highly significant. At this time, the back-transformed mean density in the control treatment was 13.14 (95% CI: 8.59, 19.07) nymphs/cm^2 while the mean densities in the three parasitoid treatments were ~1 nymph/cm^2 (Fig. 4, Table 1). The effect of treatment can be attributed almost entirely to the difference between the wasp treatments and the control. When the control treatment was removed from the analyses of the second and third sample dates, treatment no longer had a significant effect on whitefly density, suggesting that the three parasitoid treatments were equivalent (Table 1).

Despite the differences between the seasons in whitefly numbers and population trajectories, the densities of the two parasitoid species showed similar patterns in both years, although the patterns were more marked in 1998. In 1998, *E. eremicus* densities increased in the EE alone treatment but declined in the Both treatment (Fig. 5a); densities of this wasp were influenced by treatment, sample date, and the treatment-by-sample date interaction (Table 2). *Encarsia sophia* densities increased in parallel in the ES alone and the Both treatments (Fig. 5b), and only sample date had a statistically significant influence on *E. sophia* densities (Table 2).

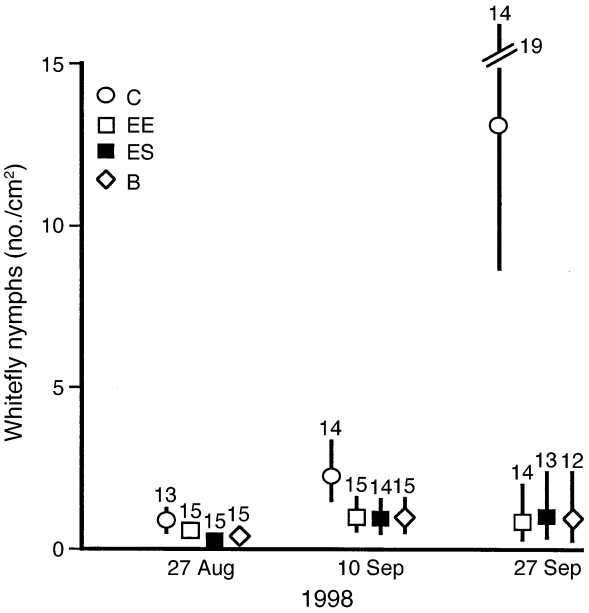

FIG. 4. Mean densities of whitefly nymphs in 1998. Key to abbreviation: C, no whitefly controls; EE, *Eretmocerus eremicus* (the primary parasitoid) alone; ES, *Encarsia sophia* (the autoparasitoid) alone; and B, both parasitoid species. Numbers above the bars are sample sizes. The means and 95% confidence intervals were back-transformed from cube-root estimates. The sample dates were analyzed separately. On both the second and third sample date, densities of whiteflies in the control treatment were significantly greater than in the other treatments (Table 1). When the control treatment was excluded, however, there was no longer a significant treatment effect (Table 1).

Total wasp densities reflected a greater population growth rate of *E. eremicus*. Wasp densities increased in the EE alone treatment, and by the time of the second and third samples, were higher than in the ES and Both treatments, while wasp densities in the latter two treatments increased only slightly (Fig. 5c). Total wasp densities were significantly influenced by treatment, sample date, and a treatment-by-sample date interaction (Table 2).

DISCUSSION

Parasitoid dynamics

The dynamics of parasitoid abundance in our experiments suggest strong asymmetric competitive effects of *E. sophia* on *E. eremicus*. In both 1997 and 1998, densities of *E. eremicus* were significantly greater in the EE alone treatment than in the Both treatment (Figs. 3a and 5a). It is possible that some of the differences in *E. eremicus* densities reflect different introduction rates (which were double in the EE treatment relative to the Both treatment); our experiment was primarily designed to detect the effects of interference competition on pest suppression rather than to document interspecific competition. However, in 1998, *E. eremicus* populations were not merely at different

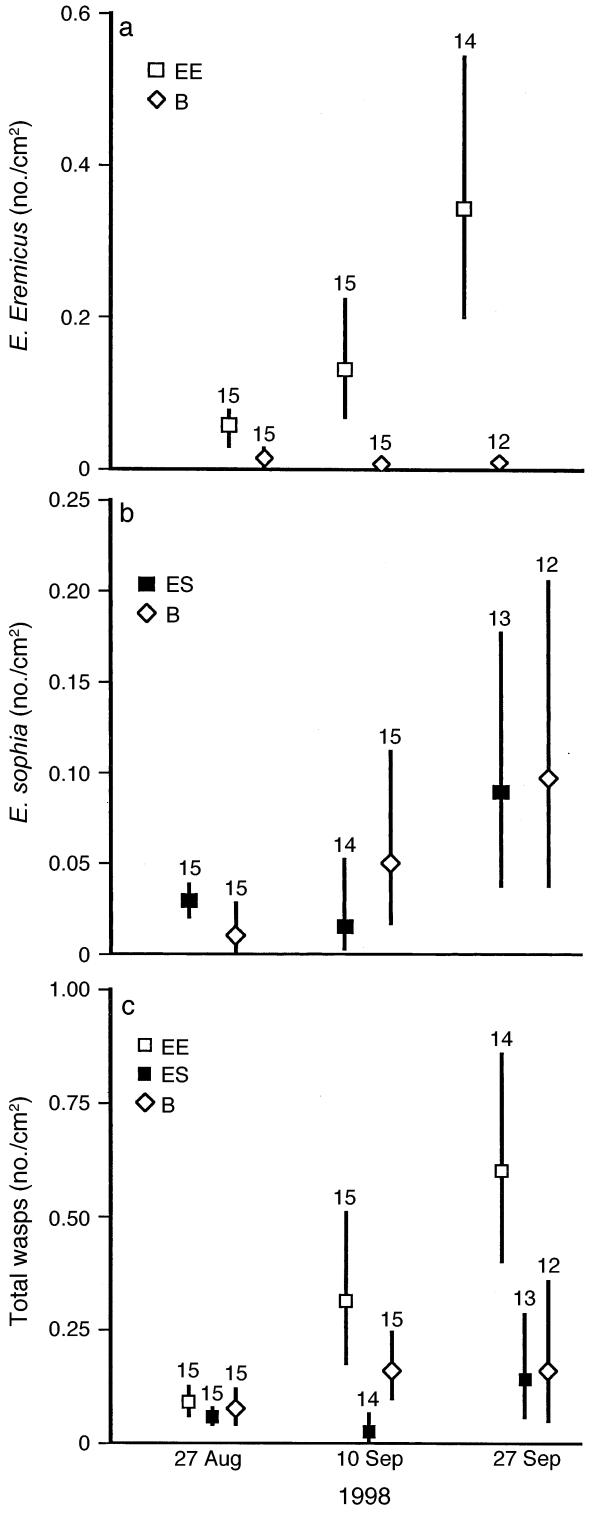

FIG. 5. Mean densities of wasp late-larval and pupal stages in 1998. Key to abbreviations: C, no whitefly controls; EE, *Eretmocerus eremicus* (the primary parasitoid) alone; ES, *Encarsia sophia* (the autoparasitoid) alone; and B, both parasitoid species. Numbers above the bars are sample sizes. The means and 95% confidence intervals were back-transformed from cube-root estimates. (a) The primary parasitoid, *E. eremicus*. Treatment, sample date, and the treatment by sample date interaction were all highly significant in their influence on the densities of *E. eremicus* (Table 3). (b) The autoparasitoid, *E. sophia*. The sample date had a significant influence on *E. sophia* densities, but treatment did not (Table 3). (c) Total wasps. Treatment, sample date, and the treatment × sample date interaction were all highly significant in their influence on the densities of total wasps (Table 3).

points along the same trajectory, as would be expected on the basis of different initial densities alone, but populations grew in the absence of *E. sophia* and declined in the presence of *E. sophia*. By the third sample of 1998, *E. eremicus* was extinct in half of the Both replicates (6/12), but not in any of the EE alone replicates (0/14). It is also clear that *E. eremicus* was more negatively influenced by the presence of *E. sophia* than the converse. In both 1997 and 1998, *E. sophia* densities were equivalent in the ES alone and Both treatments (Figs. 3b and 5b), and in the third sample of 1998, there were no replicates of either the Both treatment (0/12) or the ES alone treatment (0/14) in which *E. sophia* was extinct. That in both years *E. eremicus* densities were significantly lower in the Both treatment while *E. sophia* densities were unaffected, even in 1997 when whitefly numbers were extremely high, suggests that direct interference by *E. sophia* rather than resource limitation was responsible for the effects we observed on *E. eremicus* densities.

Strong, asymmetric competitive effects of *E. sophia* on *E. eremicus* are not unexpected given what is known about mechanisms of interference competition in these species. Hunter and Kelly (1998) found that *E. sophia* laid male eggs on and killed both *E. sophia* and *E. eremicus* immatures. *Encarsia sophia* showed no preference among suitable stages of conspecific and heterospecific immatures, but *E. eremicus* immatures were vulnerable to parasitism by *E. sophia* for twice the time that *E. sophia* immatures were vulnerable. *Encarsia sophia* pupae are enclosed within a black pupal sheath that appears to make them nearly impervious to parasitism by conspecifics. The longer vulnerability of *E. eremicus* to hyperparasitism should confer an advantage to *E. sophia* (Briggs and Collier 2001), which is consistent with the results of this study.

Other interference mechanisms may have an additional role in the competitive effect of *E. sophia* on *E. eremicus*. Collier and Hunter (2001) found that *E. sophia* interfered with *E. eremicus* via multiparasitism and host feeding on parasitized hosts. There was evidence that *E. eremicus* also won some instances of multiparasitism, but this effect was small compared to the reciprocal effect of *E. sophia* on *E. eremicus*.

The greater vulnerability of *E. eremicus* to *E. sophia* parasitism observed in the laboratory (Hunter and Kelly 1998) would lead us to predict greater parasitism of *E. eremicus* immatures than *E. sophia* immatures in the

Both treatment in 1997 when dissections were performed. While the trend was in the right direction, the difference was not statistically significant, perhaps due to the high degree of between-cage variation observed in this year. However, greater parasitism of secondary hosts in the Both treatment (including both *E. eremicus* and *E. sophia*) than in the ES alone treatment (with *E. sophia* only) is in part responsible for the significant host type-by-treatment interaction observed in the analysis of host selection by *E. sophia*. It is less clear whether the greater rate of attack on secondary hosts in the Both treatment relative to the ES alone treatment was also responsible for the lower rate of attack on primary hosts in this treatment. Presumably, either time- or egg-limitation could cause this result if females spent time or eggs on one host type and neglected the other.

Suppression of whitefly populations by parasitoids

Despite the evidence of interference competition and competitive displacement of *E. eremicus*, we found no indication of disruption of whitefly suppression in either year. Theory predicts that pest suppression may be disrupted when a more effective primary parasitoid is displaced by a less effective species that interferes with it (Rosenheim et al. 1995, Mills and Gutierrez 1996, Briggs and Collier 2001). We would not expect disruption of pest suppression in the 1997 experiment because there was no indication of effective whitefly suppression in any treatment. Whitefly densities exploded and then declined in all treatments, probably due to honeydew contamination, mold, and leaf senescence. In 1998, the parasitoid treatments were highly significantly different from the control treatment, but not different from each other. We would therefore not expect to have observed disruption of whitefly suppression in the 1998 experiment, because theory predicts no disruption if the interfering (autoparasitoid) species and primary parasitoid are equally effective at suppressing the pest (Briggs and Collier 2001).

It is possible, however, that disruption would have occurred had we carried out the experiment longer. In 1998, the most dramatic difference in total parasitoid density was seen on the last sample date; this difference might have eventually translated into greater supression of whiteflies in the EE alone treatment. We cannot judge the likelihood that disruption might have occurred later in the season after more wasp generations, which is a problem common to many experimental population dynamic studies. However, we note that in autoparasitoid competition models (Briggs and Collier 2001), disruption occurs on a similar time scale as the competitive displacement that we observed in our study.

It is surprising that the two parasitoid species suppressed host populations equivalently. There were significantly more wasps in the EE alone treatment than in the other parasitoid treatments in the last two samples of 1998. This might suggest that *E. eremicus* is more efficient than *E. sophia* at converting hosts to parasitoids, which is thought to be an indication of greater ability to suppress pest populations (Murdoch et al. 1996). It is unclear, however, what fraction of the immature parasitoids are female and it is the conversion of hosts to female progeny that is predicted to be key to effective pest suppression. Autoparasitoid–host models suggest that autoparasitoids may be more efficient at pest suppression than otherwise identical primary parasitoids because of what we call the ''sex ratio effect'' (Briggs and Collier 2001). Primary parasitoids (like *E. eremicus*) produce both male and female offspring on the hemipteran host, whereas autoparasitoids produce only female offspring. Provided that the attack rate on conspecific immatures by the autoparasitoid is not too great, autoparasitoid sex ratios can be strongly female biased and this can make an autoparasitoid species better than an otherwise equivalent primary parasitoid at suppressing pest densities (Briggs and Collier 2001). In the case of *E. sophia* and *E. eremicus*, the short window of vulnerability of *E. sophia* immatures to hyperparasitism (Hunter and Kelly 1998) and the strongly female-biased primary sex ratios of *E. sophia* (estimated to average 2% males in 1997) may have made *E. sophia* as effective as *E. eremicus* at suppressing *B. tabaci*.

Two previous studies also examined the influence of autoparasitism on parasitoid coexistence and/or host suppression. Williams (1996) found that an autoparasitoid *Encarsia tricolor* drove a sexual primary parasitoid *Encarsia inaron* to extinction in a greenhouse trial, but did not examine the effect of competition on the suppression of the whitefly host. Heinz and Nelson (1996) found that *Encarsia pergandiella*, an autoparasitoid, and *Encarsia formosa*, a parthenogenetic primary parasitoid, could suppress whitefly densities better in combination than either species could alone. However, in their study, parasitoids were released throughout the entire study period and so no competitive displacement could have occurred.

Implications for the biological control of Bemisia tabaci

It is too early to determine whether the displacement of *E. eremicus* by *E. sophia* we observed in single-plant population cages will occur in the Imperial Valley of California where *E. sophia* has recently become established. *E. sophia* coexists there with three recently introduced exotic primary parasitoids in the genus *Eretmocerus* as well as the native *E. eremicus*, and two native autoparasitoids in the genus *Encarsia*, *E. meritoria* and *E. luteola* (Coudriet et al. 1986, Roltsch 2000). There is not yet any evidence of competitive displacement of native parasitoids. One factor that may mitigate possible interference of *E. sophia* with *E. eremicus* is the tremendous spatial and temporal heterogeneity of whiteflies and parasitoids in the Imperial

Valley. The sweetpotato whitefly, *B. tabaci* has a very broad host range, and so the whitefly and its parasitoids may be found on a diverse assemblage of plants throughout the year. Theory suggests a general role for spatial heterogeneity in parasitoid–parasitoid interactions (Comins and Hassell 1996). Recent studies in other parasitoid–host systems have found conflicting results: either that local processes such as intraguild predation may be more important than a dispersal–competition trade-off in determining parasitoid coexistence (Amarasekare 2000) or the converse (Briggs and Latto 2000). The effects of spatial heterogeneity on parasitoid coexistence and pest suppression in autoparasitoid–primary parasitoid systems is at present unclear.

General implications for biological control

Autoparasitoids have been credited with dominant roles in maintaining low equilibrium pest densities in several cases of successful biological control (Smith et al. 1964, Dowell et al. 1979, Argov 1988, Nafus and Nechols 1995). Some authors, however, have expressed concern about releasing autoparasitoids because of the danger of disrupting biological control (Rosen 1981, Mills and Gutierrez 1996, Briggs and Collier 2001). We found no evidence that an autoparasitoid species disrupted whitefly suppression by a primary parasitoid species. This finding does not directly contradict theory for autoparasitoid–primary parasitoid–host interactions, however. An autoparasitoid species may not disrupt pest suppression if it suppresses the host as well (or better) than the primary parasitoid (Briggs and Collier 2001). Indeed, we found that *E. sophia* provided equal suppression to *E. eremicus*, and that both species depressed whitefly densities far below parasitoid-free conditions in one year of the experiment. Our results thus suggest that neither competitive superiority, nor inferiority at pest suppression of autoparasitoids is assured.

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