Field Evaluations of Augmentative Releases of *Delphastus catalinae* (Horn) (Coleoptera: Coccinellidae) for Suppression of *Bemisia argentifolii* Bellows & Perring (Homoptera: Aleyrodidae) Infesting Cotton

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In 1992 and 1993, field evaluations were conducted to determine the efficacy of *Delphastus catalinae* (Horn) releases for the suppression of *Bemisia argentifolii* Bellows & Perring infesting cotton in the Imperial Valley of California. Augmentative releases of adult beetles, totaling 3.5 and 5.5 beetles per plant for 1992 and 1993, respectively, were made into four 0.2-hectare cotton plots and four exclusion cages covering 40 cotton plants. Equal numbers of field plots and cages served as controls for the *D. catalinae* releases. Open field evaluations revealed no significant difference in the whitefly densities between the release and the nonrelease fields. In addition, no differences in plant growth measures were detected in the year that these data were collected. Releases of *D. catalinae* into whitefly exclusion cages resulted in a 55% and a 67% decrease in whitefly densities in 1992 and 1993, respectively. Observational data suggested that intraguild predation on *D. catalinae* by the existing predator fauna may have limited the potential for *D. catalinae* to provide biological whitefly control in open field plots relative to the levels observed within the cages. Releases of *D. catalinae* did not adversely affect population densities of indigenous parasitoids, suggesting an absence of statistically significant, antagonistic predator–parasitoid interactions. © 1999 Academic Press

Key Words: augmentation; biological control; migration; interspecific interactions; silverleaf whitefly.

INTRODUCTION

A key pest of many crops grown in the southern third of the United States is the silverleaf whitefly (Perring *et al.,* 1993), *Bemisia argentifolii* Bellows & Perring (Homoptera: Aleyrodidae) (= strain B of *Bemisia tabaci* [Bellows *et al.,* 1994]) (Brazzle *et al.,* 1997; Toscano *et al.,* 1998). In Florida, Texas, Arizona, and California, damage to crops in 1991 and 1992 was estimated at

$200 and $500 million, respectively (Henneberry and Toscano, 1996). Growers have adjusted agricultural practices to cope with the whitefly but costs for insecticides to control the pest remain high. Whitefly control costs for 1993 were estimated to exceed the $18.9 million 1992 costs (Henneberry and Toscano, 1994). Growers in California's Imperial County spent roughly $12 million in 1996 to protect 49,442 acres of melons from silverleaf whitefly (White, 1998).

In addition to its economic costs, reliance on periodic applications of insecticides for management of *Bemisia* spp. cause other problems. One problem is the development of widespread resistance and cross-resistance of whiteflies to many commonly used conventional insecticides, particularly organophosphates and synthetic pyrethroids (Prabhaker *et al.,* 1985; Horowitz *et al.,* 1988; Dittrich *et al.,* 1990; Bloch and Wool, 1994). Resistance to the insect growth regulators buprofezin and pyriproxyfen has also been reported (Horowitz and Ishaaya, 1994). Resistance to insecticides, concerns about environmental toxicity (Bascietto *et al.,* 1990), and danger to worker safety (Maddy *et al.,* 1985; Hock, 1987) mandate the development of alternatives to conventional chemical control of whitefly.

Biological control has great potential for use against silverleaf whitefly, based on successes of biological control against other introduced whitefly species and the abundance of potential biological control agents. In California, there are at least 8 species of exotic whiteflies, of which 4 are managed with the help of biological control (DeBach and Rose, 1976; Rose and DeBach, 1981; Miklasiewicz and Walker, 1990; Bellows *et al.,* 1992; Gould *et al.,* 1992; Metcalf and Metcalf, 1993). As for the *Bemisia* complex, many potential natural enemies have been identified, including 37 parasitoid species, mainly in the genera *Eretmocerus* (Howard) and *Encarsia* Förster, and 34 predators, in the families Coccinellidae and Phytoseiidae (Cock, 1986, 1993; Gerling, 1986, 1990).

Most work on the biology and utilization of whitefly natural enemies in biological control programs has involved parasitoids (Gerling, 1992; Onillion, 1990). Recently, new attention has been given to predators as potential agents for control of *Bemisia* spp. (as reviewed by Nordlund and Legaspi, 1996; Obrycki and Kring, 1998). The few greenhouse and field studies aimed specifically at testing predators for biological control of *Bemisia* (Breene *et al.,* 1992; Gerling *et al.,* 1997) have produced variable results.

Laboratory and greenhouse preintroduction evaluations of adult longevity, prey consumption, and fecundity as a function of *B. argentifolii* density have been used successfully to eliminate species found to be poorly adapted for use in *B. argentifolii* biological control programs (Heinz and Parrella, 1994a, 1998; Heinz, 1996). Results from comparisons among 14 species of parasitoids and predators suggested that *Delphastus catalinae* (Horn) may be a superior biological control agent for *B. argentifolii* (Heinz, 1996). Subsequently, Heinz and Parrella (1994b) demonstrated that the combined release of *Encarsia luteola* Howard and *D. catalinae* (which was misidentified as *Delphastus pusillus* LeConte prior to the taxonomic work of Gordon [1994]) successfully controlled *B. argentifolii* infesting poinsettias, *Euphorbia pulcherrima* Willd., in commercial production greenhouses.

Delphastus spp. are active whitefly predators throughout their long adult life (Hoelmer *et al.,* 1994); both male and female beetles exhibit high prey consumption rates (Heinz and Parrella, 1994a; Hoelmer *et al.,* 1993), and females are highly fecund (Heinz *et al.,* 1994). In addition, they exhibit partial compatibility with the indigenous parasitoid species resulting from their preference for preying on healthy whitefly or their inability to prey on parasitized whitefly in their later stages of development (Heinz *et al.,* 1994; Hoelmer *et al.,* 1994). These traits suggest that *D. catalinae* may be a good biological control candidate for use in agroecosystems with high whitefly densities.

To test this hypothesis, field evaluations were conducted to determine the efficacy of inundative releases of the whitefly predator *D. catalinae* for biological control of *B. argentifolii*. Specific objectives were to examine the survival and reproduction of *D. catalinae* under field conditions, to evaluate the predator's effectiveness in suppressing *B. argentifolii* populations infesting cotton, and to observe the interactions of this introduced predator with indigenous parasitoids of *B. argentifolii*.

MATERIALS AND METHODS

Experimental field sites. This study was conducted during 1992 and 1993 at the University of California Desert Research and Extension Center (UCDREC), El Centro, California. The experimental plots consisted of eight, 0.2-hectare fields of *Gossypium hirsutum* L. var. DP 5461 planted on 5 May 1992 and 3 May 1993. These plots were maintained following standard commercial practices with the exception that no insecticide applications were made. All plots were spatially separated throughout the UCDREC with a minimum interplot distance of 0.4 km to prevent cross-contamination among plots. Composition of the surrounding vegetation was variable, ranging from fallow land to alfalfa (*Medicago sativa* L.), Sudan grass (*Sorghum sudanense* [Piper] Stapf), beans (*Phaseolus* sp.), and other cotton fields. A 8.2-m-wide border of cotton was maintained around the outer perimeter of each plot to minimize edge effects.

A $2 \times 2 \times 1.9$ m exclusion cage, covering approximately 40 cotton plants, was randomly placed in each of the eight experimental plots on 14 July 1992 and 18 June 1993. At these times plants were host to dense whitefly populations in both years. The exclusion cages were constructed of a schedule 40, PVC pipe frame covered with Lumite 42×42 mesh with openings of 350 μm (Lumite Corp., Gainesville, GA). This material provided 100% exclusion of *B. argentifolii* adults (Bethke and Paine, 1991), eliminating any further migration. Adult *D. catalinae* movement was also restricted by the cages; however, the whitefly parasitoids were likely able to penetrate through the fabric. To determine the effect of the cages on temperature, a two-channel temperature recorder (Omnidata Model DP212 with a DSM1000 data storage module and TP10V temperature probe; Omnidata International, Logan, UT) was used to monitor hourly temperatures within the cotton canopy from both inside and outside of one cage in each treatment in 1992 and 1993. Temperature data could not be retrieved from one data recorder in 1992 due to equipment failure; therefore, no temperature comparisons were made for 1992.

Four of the eight open field plots and cages received releases of *D. catalinae* while the other four plots and cages acted as experimental controls and received no *D. catalinae* releases. Each cage received the same treatment designation as its surrounding field plot. This design allowed for simultaneous testing of the efficacy of *D. catalinae* releases under normal field conditions and under conditions in which whitefly migration was eliminated.

Delphastus catalinae releases. All *D. catalinae* beetles used in this study were reared on *B. argentifolii* infesting poinsettia plants in greenhouses located at the California Department of Food and Agriculture's Biological Control unit in Sacramento, California (see Pickett *et al.,* 1999 for details). Approximately half of the adult beetles within the mass-rearing facility were harvested every 1–3 weeks for release into the field. Allotments of 500 adult beetles of unknown age were

placed into 0.5-L plastic bottles and shipped in a cooled ice chest by next-day service to the UCDREC. Two days elapsed between collection and subsequent release into experimental plots.

On 4 July 1992 and 16 June 1993 the number of plants per plot and cage were counted to insure equal release rates (beetles per plant) among the four release plots and cages. In 1992, releases of adult *D. catalinae* began on 21 July and continued through 19 August in the field plots and through 17 September in the cages. In 1993, releases began 19 June and continued through 4 August in both the open field plots and cages. A total of 35,144 beetles (3.5 beetles per plant) in 1992 and 76,784 beetles (5.5 beetles per plant) in 1993 were released. Beetles were released by gently shaking them from the bottles onto approximately 20% of the plants prior to 9 am the morning after their delivery to the UCDREC.

Sampling. Whitefly population densities and the impact of natural enemies were monitored weekly following a stratified random sampling plan (Southwood, 1978). Each open field plot was divided into 20 equal blocks and each cage into 4 equal blocks. One plant within each block was then arbitrarily selected, from which a vertically stratified leaf sample was collected. The vertically stratified sample consisted of removing mainstem leaves (Von Arx *et al.,* 1984) every 10 cm along the central stem of each cotton plant to obtain leaf samples of different ages and microenvironments. This protocol, in turn, increased the probability of detecting unbiased changes in whitefly and natural enemy population densities and provided a measure of the densities of all whitefly stages (Natwick *et al.,* 1996; Naranjo, 1996).

Weekly leaf sampling in 1992 began 14 July and ended 26 August in the open field plots and 14 October in the cages. On 1 September open field plots were plowed under in compliance with Imperial County's cotton boll termination regulations. Therefore, the final field sample was collected 26 August 1992. In 1993, sampling began on 18 June, approximately 1 month earlier than in 1992. Final samples were collected in the open field plots on 19 August and in the cages on 31 August.

Leaves were refrigerated at 4–5°C until processing, which was completed within approximately 10 days of sampling. The leaf samples were taken to the laboratory where two 0.75-cm² leaf punches were extracted from the proximal section of the two leaf sectors most distal to the petiole (as described by Von Arx *et al.,* 1984; Ohnesorge and Rapp, 1986; Naranjo and Flint, 1994). Use of the leaf punches as a subsample was necessary to quantify very large whitefly populations in a timely manner, thus increasing the number of leaves that could be sampled. The numbers of whitefly eggs and live and parasitized immature whiteflies were

recorded from the two leaf punches with the aid of a dissecting microscope. A parasitized whitefly was classified by the swollen condition of the whitefly nymph in conjunction with disruption of the integrity of the mycetomes or by the visual presence of a developing parasitoid within the whitefly. For *Encarsia* spp., the presence of meconia was used as an identifying character (Gerling, 1990). A limited number of the parasitoids were reared out for identification at the generic level.

D. catalinae populations were monitored throughout the 1992 and 1993 studies to detect signs of survival, development, and reproduction under field conditions. The abundance of *D. catalinae* eggs per cm² of leaf tissue was determined using the leaf samples described above. In addition, the abundances of larvae, pupae, and adults were estimated by timed searches (insects per minute) in both the open field plots and the cages. Random walks were made through each field while visually inspecting as much of the plants' surfaces as possible. Although search times were arbitrarily set at 30 min per open field plot and 2 min per cage, these search times represented approximately equal amounts of search time per area searched.

To determine the impact of *D. catalinae* releases on plant growth and potential yield, measurements of plant height and boll formation in the open field plots were taken at the end of the 1993 study following previously described methods (IPM Manual Group, 1984). Ten arbitrarily selected plants per replicate (40 plants per treatment) were measured to determine the mean height per treatment. Potential yield was determined from the mean numbers of cotton bolls obtained from counts made on cotton plants within 10 arbitrarily selected 1-m sections of row per replicate.

Whitefly movement. In 1993, yellow sticky traps were used to measure whitefly dispersal to and from the experimental plots. The traps (8.1 × 9.9 cm) were stapled to the bottoms of clear plastic entrée platters (21.8 × 13.0 × 4.4 cm) with fluted sides. Two sticky traps were placed on a stake with one trap facing the research plot and other facing away to monitor both emigrating and immigrating whiteflies. The tops of the traps were placed at heights approximately equal to heights of the cotton plants (Melamed-Madjar *et al.,* 1979, 1982). Traps were placed 1 m from each of the four sides of the field, a distance ensuring that emigration levels were not artificially inflated by attracting whiteflies out of the field (Cohen, 1982). Once weekly, whitefly populations were trapped during a 24-h period. Cards were then returned to the laboratory and the number of adult whitefly captures was determined using a dissecting microscope. Net whitefly immigration or emigration within a field was estimated as the difference between the pooled trap catches among the outward- and inward-facing traps.

Statistical analyses. The effects of the *D. catalinae* releases on whitefly and parasitoid densities were analyzed by comparing the mean *B. argentifolii* and immature parasitoid densities in the release versus the nonrelease areas. Densities were standardized to 1 cm² of leaf tissue and the means were weighted by the number of leaves within each sample per replicate. Between-treatment variation in population densities among open field plots and exclusion cages was analyzed using a repeated-measures analysis of variance (ANOVA) (Statsoft Inc., 1993) with sample date as the repeated measure.

Among-treatment comparisons of the mean number of immigrating and emigrating whitefly adults were performed using a repeated-measures ANOVA (Statsoft Inc., 1993). Immigrating and emigrating whitefly adults were pooled per replicate. Migration measurements were taken in four release fields yielding four replicates per treatment (movement in or out of the field). The effect of time and the interaction of treatment by time were included within the ANOVA to test for differences in whitefly densities and treatment differences across sample dates.

In addition to data collected on insect densities, plant growth and temperature data from 1993 were also available for analyses. The mean plant height and number of bolls among each of the four release and nonrelease treatments were analyzed using a one-way ANOVA (Statsoft Inc., 1993). A two-way ANOVA (Statsoft Inc., 1993) was used to detect whether temperatures within exclusion cages differed significantly from temperature outside the cages across sample times.

A predictive model was used to estimate the effect temperatures have on *B. argentifolii* development. Recorded temperatures were converted to degree days per day based upon a lower threshold of 10°C and an upper threshold of 32°C (Zalom *et al.,* 1985). The degree days per day estimated inside and outside the exclusion cages were then compared using a two-way ANOVA (Statsoft Inc., 1993). In the ANOVA model, the effect of time and the interaction of treatment by time were examined to test for degree day and treatment differences across sample dates. Degree-day values were subjected to a $\log_{10}(x + 1)$ transformation to normalize data prior to analysis.

RESULTS

Delphastus catalinae densities. Beetle larvae, pupae, and adults were never observed in leaf samples or time counts taken in 1992 or 1993. Hence, all *D. catalinae* collected were a direct result of the releases made to the treatment plots. Also, beetle dispersal between treatments was below levels detectable by our sampling methods.

In 1992, timed searches detected *D. catalinae* larvae as early as 4 August in the cages and 10 August in the open field plots (15 and 21 days after the first release, respectively). Pupae and teneral adults were first observed in 1992 on 10 August in both the open field plots and cages (Fig. 1). Teneral adults were identified by their light brown color, characteristic of beetles in the latter stages of ecdysis before complete melanization of the procuticle. Larval and pupal populations of *D. catalinae* comprised 12 to 88% of the total population on each search date after 10 August, inclusive.

During 1993, *D. catalinae* were first recovered on 22 June, 3 days after the first release date, in both the open field plots and cages. Beetle larvae first were observed in the field plots on 29 June and beetle pupae and newly emerged adults on 4 August (Fig. 1). *D. catalinae* larvae appeared in the cages on 8 July, and beetle pupae and newly emerging adults were observed on 28 July (Fig. 1). Larval and pupal populations comprised 21 to 96% of the total population on each search date after 8 July, inclusive. These high proportions of immature *D. catalinae* are similar to those observed for 1992. Copulating adults and the presence of *D. catalinae* eggs, larvae, and pupae were observed in the field during the collection of leaf samples throughout the 1992 and 1993 studies. These results show that *D. catalinae* can survive, develop, and reproduce in an environment in which summer temperatures often exceed 42°C.

Whitefly densities: 1992 study. The open field treatments show no significant difference ($F = 0.01; df = 1,6; P = 0.993$) in whitefly densities between the release and the nonrelease plots (Fig. 2). In the release plots, *D. catalinae* populations were not detected until late in the study, 10 August 1992, and peaked at 0.33 beetles per minute of searching (Fig. 1). The lack of significant whitefly suppression may be a result of the low *D. catalinae* densities.

In the cage plots, *D. catalinae* populations increased substantially beginning 2 September. Beetle populations remained low through 26 August, after which a 20-fold increase in the overall population was observed (Fig. 1). This increase in the *D. catalinae* population corresponds with significant suppression of the whitefly populations in the release cages beginning 9 September. On the last sampling date, whitefly densities were 55% smaller in the release than in the nonrelease cages (Fig. 2). A significant difference ($F = 13.99; df = 1,6; P = 0.009$) in whitefly densities between the release and the nonrelease cages was observed across sample dates. The increase in whitefly densities over time was significant ($F = 6.33; df = 13,78; P < 0.001$). A significant treatment × time interaction ($F = 5.35; df = 13,78; P < 0.001$) was also observed. This significant interaction was presumably due to similar whitefly densities in the two treatments at the start of the trial and significantly fewer whiteflies in the *D. catalinae* release
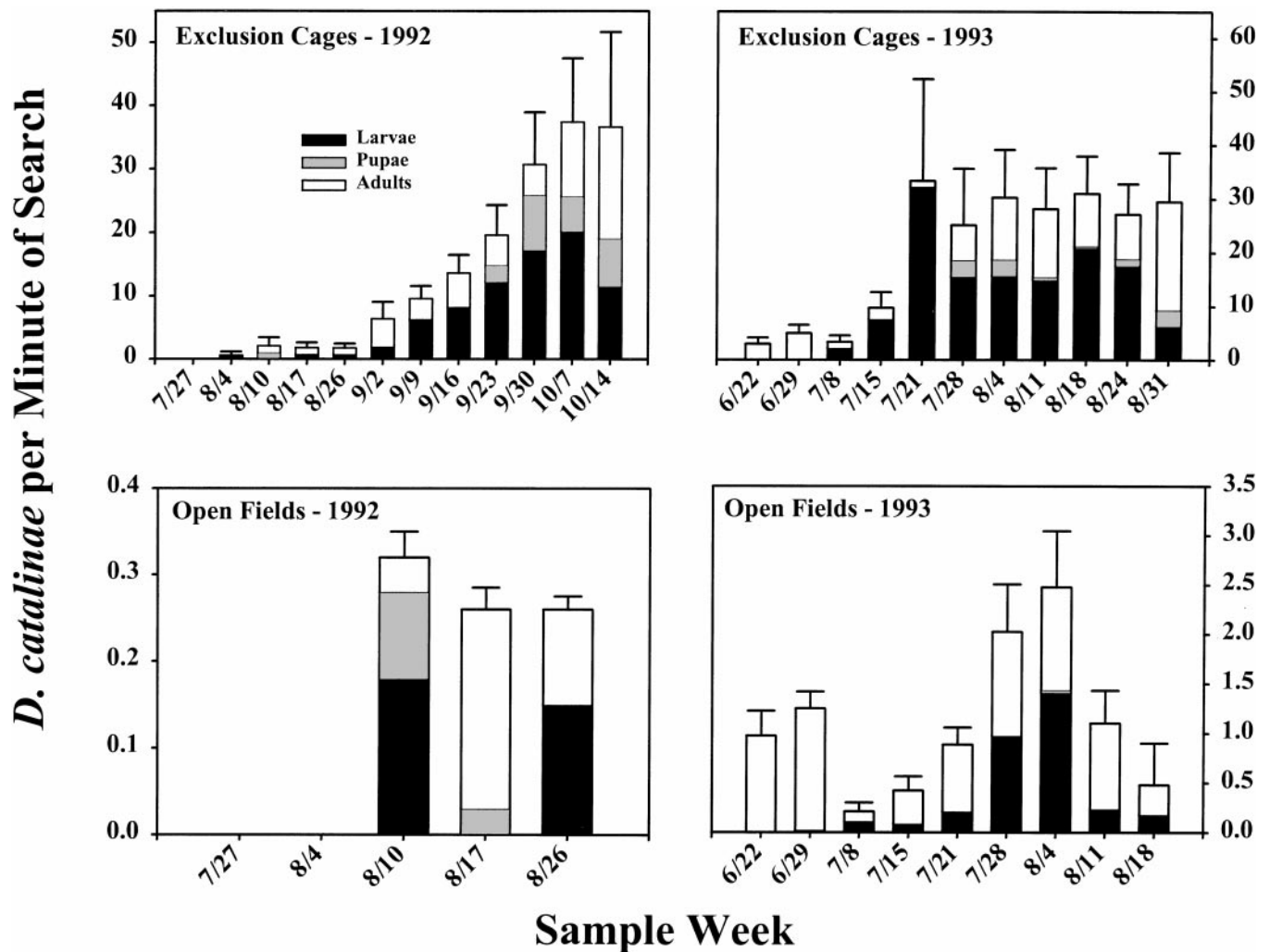
FIG. 1. Mean numbers of *Delphastus catalinae* observed per minute of searching in the 1992 and 1993 exclusion cages and open fields ($N = 4$ replicates per treatment per year). Total search time was 2 min within the exclusion cages and 30 min in open field. Standard error bars based upon total beetle populations are shown.

treatment compared to the nonrelease treatment at the end of the trial (Fig. 2).

A delay in *D. catalinae* population growth and subsequent suppression of whitefly densities in the release cages suggests that early season releases of the predator may suppress whitefly populations before they reach uncontrollable levels. For example, in 1992 whitefly densities had already reached 60 immature whiteflies per cm² of leaf area before the first release. In an effort to enhance whitefly control, *D. catalinae* releases were begun >30 days earlier in 1993 compared to the initial release date for 1992.

Whitefly densities: 1993 study. Higher average densities of *D. catalinae* developed in 1993 (Fig. 1) than in 1992. In the open field plots, *D. catalinae* populations steadily increased from 8 July and through 4 August. However, the higher beetle populations observed in 1993 (Fig. 1) did not result in better control of whitefly

populations in the open field plots (Fig. 2). Similar to 1992, no significant difference in whitefly density was observed between the release and the nonrelease, open field treatments ($F = 0.04$; $df = 1,6$; $P = 0.855$).

In the 1993 release cages, *D. catalinae* populations peaked on 21 July and remained slightly below this level until the end of the study (Fig. 1). On 10 August, 20 days after this peak, significant reductions in whitefly densities were observed in the release treatments (Fig. 2). On the last sampling date, whitefly densities were 65% smaller in the release cages than in the nonrelease cages. A significant treatment effect ($F = 6.42$; $df = 1,6$; $P = 0.044$) was observed in the whitefly densities between the release and the nonrelease cages. In addition, time ($F = 7.39$; $df = 10,60$; $P < 0.001$) and interaction of treatment by time ($F = 4.73$; $df = 10,60$; $P < 0.001$) effects were significant.
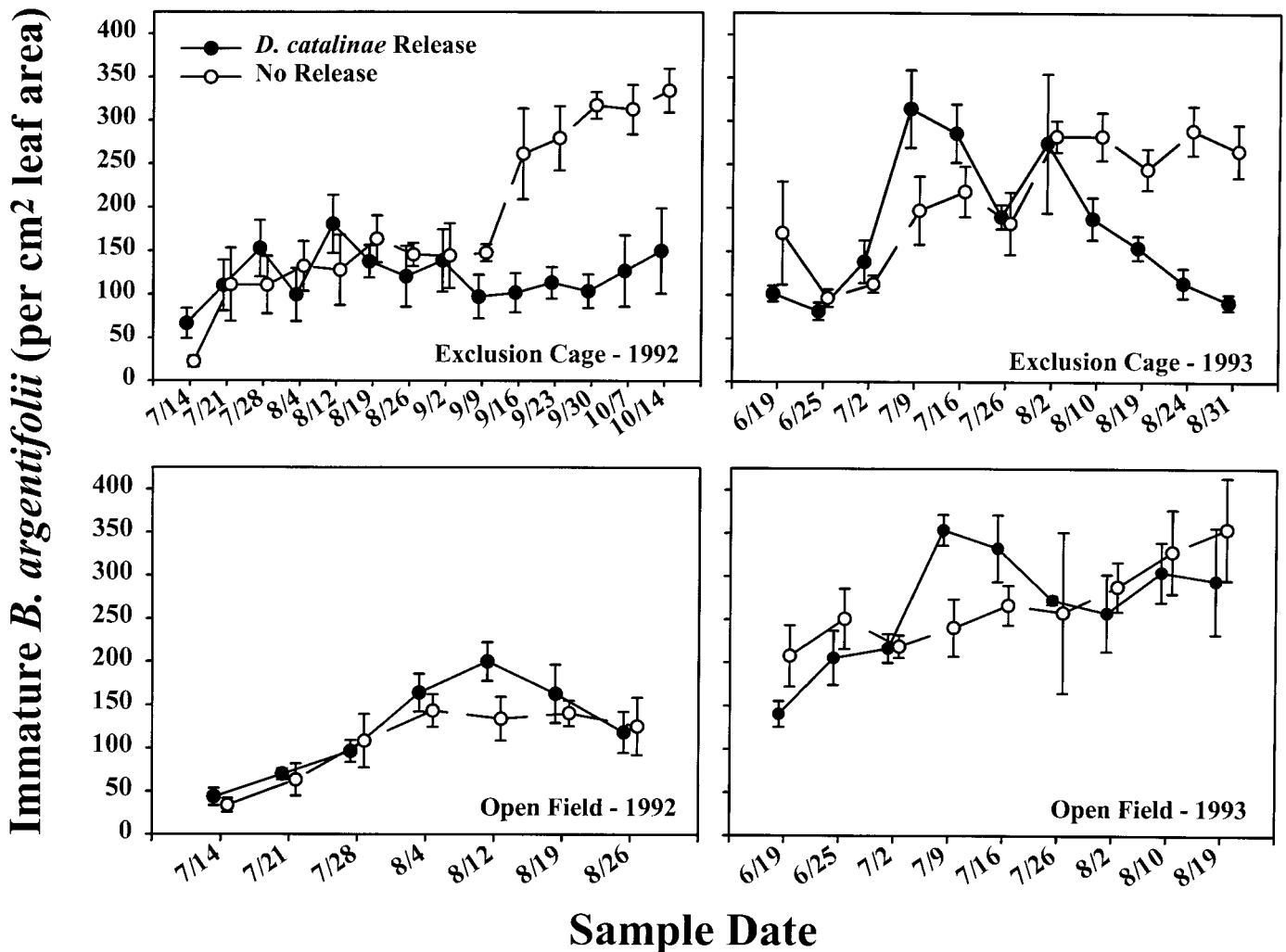
FIG. 2. Densities of immature *Bemisia argentifolii* in the 1992 and 1993 exclusion cages and open fields (*N* = 4 replicates per treatment per year). The x-axis represents the week samples were taken, and the y-axis represents the number of *B. argentifolii* (eggs + nymphs + pupae) per cm² of leaf area. *B. argentifolii* densities are expressed as the means ± 1 SEM (vertical bars).

The lack of whitefly suppression in the open field plots was also apparent from the plant growth measurements. No significant differences were observed for the 1993 plant growth measurements. Plant height ($F = 0.36$; $df = 1,6$; $P = 0.569$) and the number of bolls ($F = 2.32$; $df = 1,6$; $P = 0.178$) did not differ in the release compared to the nonrelease open field plots.

Whitefly movement. Movement of *B. argentifolii* in and out of the experimental plots was monitored with yellow sticky cards throughout the 1993 study. Comparison of immigrating and emigrating whiteflies across all sample dates revealed no significant difference ($F = 0.82$; $df = 1,190$; $P < 0.366$). A net immigration of 745, 538, and 444 whiteflies per sticky card per 24-h period was observed for the 3 weeks immediately following the first *D. catalinae* release (Fig. 3). These immigrations were countered by net emigrations of >550 whitefly for the next two sample dates, 20 and 27

July. A second pulse of immigrating whitefly adults was observed over the last two sample dates (Fig. 3).

Temperature. Mean daily temperatures recorded during the 1993 study (Table 1) were significantly greater outside than inside the exclusion cages ($F = 29.25$; $df = 1,140$; $P < 0.001$). Temperature increased significantly with time throughout the study ($F = 467.68$; $df = 1,140$; $P < 0.001$). Changes in daily temperatures, however, were consistent between treatments as indicated by the lack of a significant interaction term ($F = 0.78$; $df = 69,140$; $P = 0.873$).

The potential influence of these differential temperatures on whitefly population growth was determined by converting temperatures to whitefly heat units based upon the degree-day model developed for *B. tabaci* (Zalom *et al.*, 1985). Calculated degree-day accumulation per day revealed significantly greater values in the exclusion cages compared with the open field plots
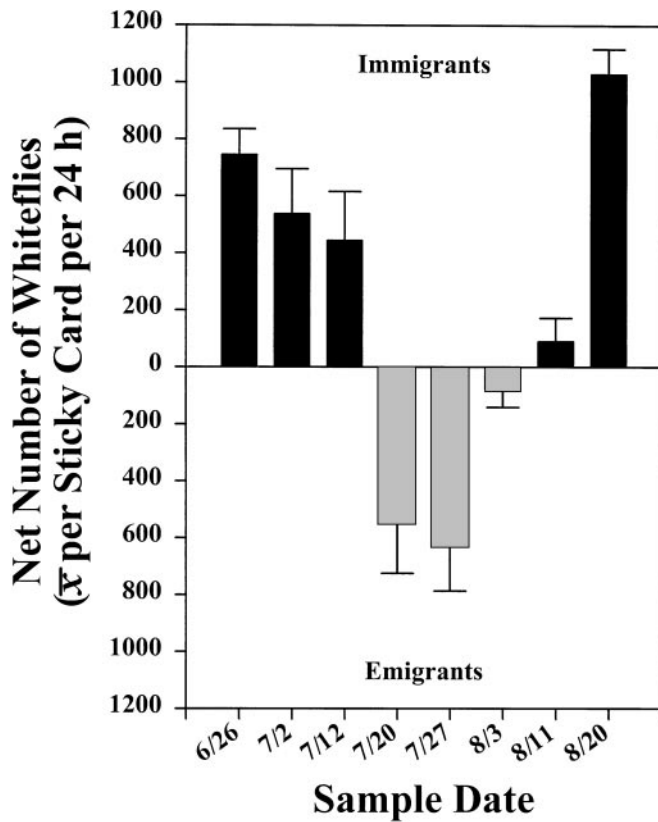
FIG. 3. Mean numbers of net immigrating and emigrating whitefly for each date sampled. The average numbers (±1 SEM) of whitefly caught on an 80-cm^2 yellow sticky card within a 24-h period (four cards per replicate, four replicates per treatment per sample date) are plotted against the dates that cards were placed along the perimeter of the *D. catalinae* release plots.

($F = 62.19; df = 1,140; P < 0.001$) (Table 1). Mean daily temperatures in the open field plots often exceed the upper temperature threshold for whitefly development, resulting in lower degree-day accumulation. Degree-day accumulation fluctuated over the length of the season within the bounds of the upper and lower thresholds but because temperatures in the open field plots frequently exceeded the upper temperature threshold, a significant time by treatment interaction was

TABLE 1

1993 Mean Daily Temperatures and Degree-Day Accumulations within the Open Field Plots and Exclusion Cages in Two of the Experimental Plots

Treatment	Temp °C, $\bar{x}$ mean ± SE	°D per day, $\bar{x}$ ± SE
Exclusion Cages	30.20 ± 0.02 a	16.25 ± 0.75 a
Open Field Plots	32.05 ± 0.03 b	11.50 ± 1.00 b

Note. Values within columns followed by different letters are significantly different at P = 0.01.

observed ($F = 7.35; df = 69,140; P < 0.001$). The degree-day accumulation values suggest that whitefly development rate and population growth should be faster in exclusion cages than in open fields.

Interactions with indigenous parasitoids. Densities of immature *Encarsia* and *Eretmocerus* spp. were monitored throughout the 1992 and 1993 studies to determine potential compatibility with *D. catalinae*. *Eretmocerus* spp. comprised >90% of the parasitoids identified from the leaf samples. Densities of immature parasitoids in the open fields increased with each sample date as the season progressed, with the exception of the final sample date (Fig. 4). There were no obvious population-level trends for immature parasitoids in the exclosure cages among years. No significant differences in immature parasitoid densities were detected when comparing populations from the release and nonrelease treatments from either the open field plots or exclosure cages (Table 2). These results are consistent with the hypothesis that *D. catalinae* had no apparent adverse effects on the indigenous parasitoid populations.

DISCUSSION

Results of this study suggest that *D. catalinae* can survive, develop, and reproduce in the Imperial Valley during the cotton-growing season. Total generation time observed in the field was approximately 19–20 days from release onto the plants to adult emergence. Copulating *D. catalinae* adults, their eggs, and large populations of larvae were observed throughout the high-temperature periods recorded during the study. Thus, beetles reared on poinsettias within a greenhouse located in Sacramento, California successfully adapted to the conditions associated with cotton production in the Imperial Valley.

Whitefly populations encountered during the studies were very high, ranging from 22 to 334 whiteflies per cm^2 of leaf area in 1992 and 97 to 350 whiteflies per cm^2 of leaf area in 1993. Because plants were colonized by high numbers of whitefly prior to the initiation of the studies, accomplishing any level of biological control prior to termination of the crop was difficult. In 1993, earlier releases were planned in an effort to attack whitefly populations at lower densities. Implementation of this strategy translated into higher *D. catalinae* densities earlier in the season but did not translate into greater whitefly suppression. Higher whitefly densities prior to *D. catalinae* releases likely negated the benefits of the earlier releases in 1993 compared to 1992. Whitefly densities were approximately three times greater in the open field plots and two times greater in the cages in 1993 compared to 1992.

D. catalinae releases into the exclosure cages during the 1992 and 1993 studies significantly reduced whitefly population densities to less than one-half the densi-
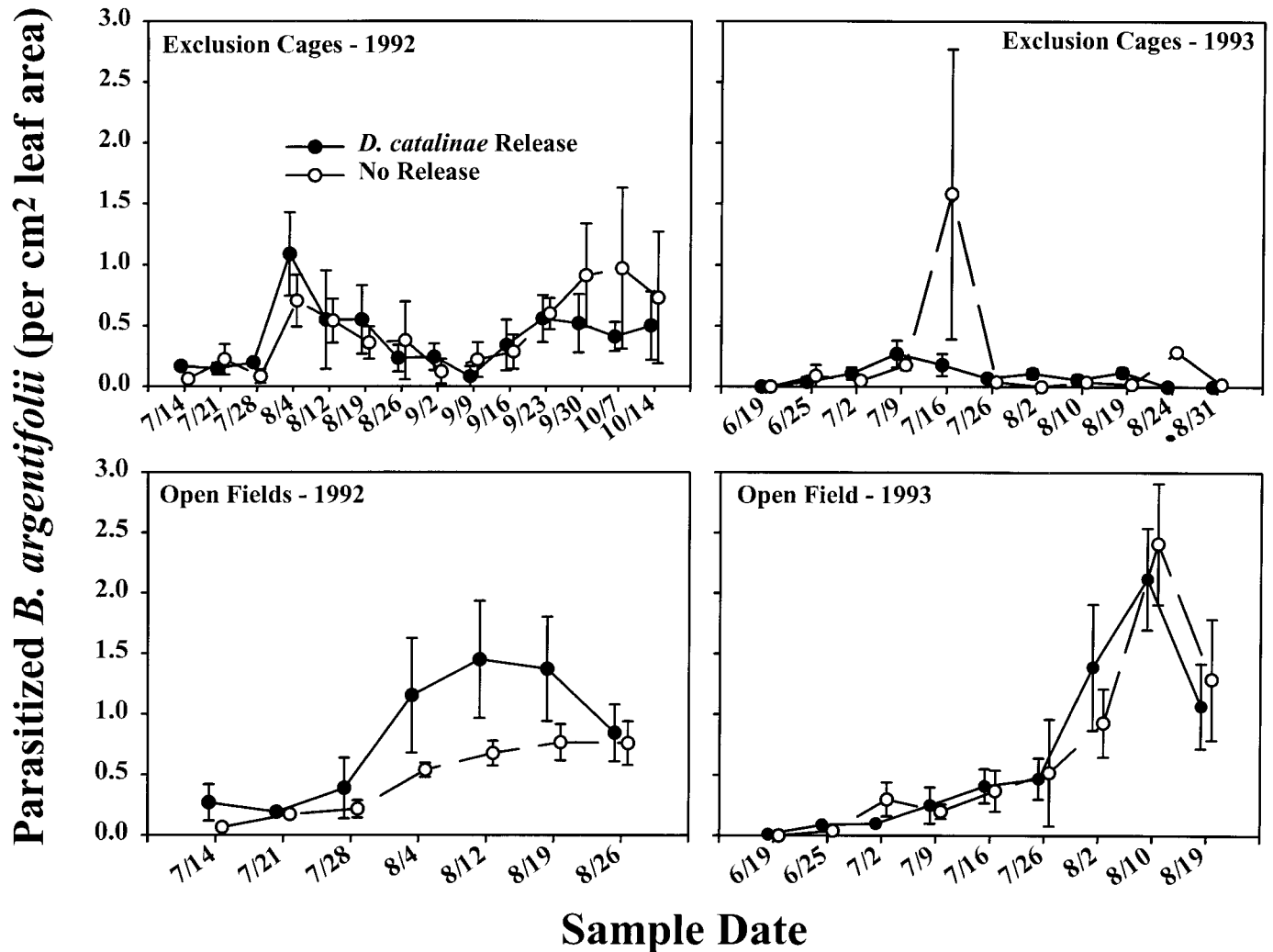
FIG. 4. Average densities of immature parasitoids (±1 SEM) collected in weekly samples taken in 1992 and 1993 from the exclusion cages and open fields (*N* = 4 replicates per treatment per year).

ties observed in the nonrelease cages. Although reduction of whitefly densities was substantial, densities were still well above the frequently used action threshold of 5–10 adult whitefly per leaf (Ellsworth, 1995). In the open field plots, *D. catalinae* did not significantly reduce the whitefly densities in 1992 or 1993. Several explanations exist for the differential results between the open field plots and the cages.

The pattern of whitefly movements varied greatly with time but no significant differences in the total numbers of emigrating or immigrating whitefly were detected (Fig. 3). Because net immigration into cotton fields was large during the early phases of the study (Fig. 3), the level of biological control was expected to be enhanced by the elimination of whitefly movement into the release cages. However, whitefly densities in the exclosure cages were quite similar to the densities in open field plots (Fig. 2), arguing against a significant

role of whitefly immigration. In terms of the importance of whitefly migration on the success of biological control, our results do not support reports from other studies conducted in the Imperial Valley. Minkenberg *et al.* (1994) and Simmons and Minkenberg (1994) noted the level of biological control to be greater in the absence of whitefly migration, although the levels of whitefly migration were never actually measured in either of the studies.

Degree-day accumulation estimates suggest that the whitefly exclusion cages may have influenced population growth of *B. argentifolii*. Development of *B. argentifolii* was predicted to be more rapid in the cages, based upon the larger degree-day values in the cages compared to those in the open field plots. Therefore, whitefly densities in the nonrelease cages should have been greater than those observed in the open field control plots, in the absence of other contributing

TABLE 2

1992 and 1993 Analyses of Parasitized Whitefly Immatures in the Release versus Nonrelease Treatments

Year	Treatment	Parasitized whitefly immatures per cm^2, $\bar{x} \pm SE$[a]	F[b] ($df = 1,6$)	P[b]
1992	Exclusion cages (release)	0.40 ± 0.07		
	Exclusion cages (no release)	0.44 ± 0.08	0.05	0.837
	Open field plots (release)	0.81 ± 0.20		
	Open field plots (no release)	0.45 ± 0.11	1.95	0.212
1993	Exclusion cages (release)	0.10 ± 0.02		
	Exclusion cages (no release)	0.15 ± 0.07	0.77	0.414
	Open field plots (release)	0.66 ± 0.24		
	Open field plots (no release)	0.67 ± 0.25	0.02	0.961

[a] Means were pooled across all sample dates.
[b] Values derived from a two-way ANOVA: repeated measures.

factors. In fact, whitefly densities were greater in the open field control plots, which may be due to the overwhelming effect of early season migration of whiteflies into the open field plots.

There are other potential explanations for the variable results observed between the cage and the field releases, and these include the dispersal behavior of *D. catalinae* adults and predation by generalist predators on *D. catalinae*. Although the cage treatments were included in this study to eliminate whitefly movement, they also acted as a barrier to the movement of *D. catalinae* and existing generalist predators. The inclusionary effect of the cages on *D. catalinae* adults may have contributed to the variability in their population growth and subsequent suppression of *B. argentifolii*. Coccinellids show a high propensity to disperse dependent upon the availability of prey and temperatures (Ives, 1981). However, based upon the high prey densities observed throughout the studies (greater than 50 whitefly immatures per cm^2 of leaf area), prey availability does not appear to be an issue. Experiments examining the dispersal behavior of *D. catalinae* in alfalfa fields in the Imperial Valley concluded that adult beetles released from a central point source dispersed less than 1 m/day at prey densities similar to those observed in this cotton study (K.M.H. and J.R.B., unpublished data). This low propensity to disperse suggests that movement of *D. catalinae* out of the experimental plots was probably minimal.

While the direct effects of generalist predators were not measured quantitatively, qualitative field observations suggested that levels of generalist predators in the open field plots were greater than the levels observed in the cages. Predators observed included *Orius* and *Geocoris* spp. feeding on the eggs of *D. catalinae; Zelus* and *Sinea* spp. feeding on late instar larvae and adults; and *Nabis, Chrysoperla, Hippodamia* spp., and several unknown species of spiders and ants feeding on *D. catalinae* larvae and adults. These direct field observations suggested that *D. catalinae* mortality by indigenous predators may have been significant, especially in the open field plots. These negative predator–predator interactions may have reduced greatly the ability of *D. catalinae* releases to effect biological whitefly control.

No adverse interactions between *D. catalinae* and indigenous whitefly parasitoids were detected. Differences in prey acceptance or mechanical inability to feed on parasitized whiteflies by *D. catalinae* may produce a compatibility that can be utilized as a part of a multiple-species release program (Heinz *et al.,* 1994; Heinz and Parrella, 1994b). These interactions with the whitefly parasitoids, which include *Encarsia transvena* (Timberlake), *Eretmocerus* nr. *californicus* (Hoelmer *et al.,* 1994), and *Encarsia pergandiella* Howard (Nelson and Parrella, 1993; Heinz *et al.,* 1994), have been studied under laboratory conditions as well. These studies concluded that *Delphastus* adults avoid or are unable to feed on parasitized whiteflies in advanced stages of development.

One of the main limitations to cheap and efficient biological control is the inability to preselect natural enemies and determine their future qualities as controlling agents prior to their field utilization (Gerling, 1992). As a result of the constraints on resources, much of the necessary selection in this process is arbitrary and not related to any aspect of an agent that might indicate its potential value (Waage, 1990). *B. argentifolii* is a good example for which the sense of urgency for natural enemies limits and in some cases eliminates preintroduction studies. Although the validity of this reductionist approach has often been debated (Ehler and Andres, 1983; Waage, 1990), before this field study we embraced this approach to identify 1 potentially superior biological control agent from 14 candidate species (Heinz and Parrella, 1994a, 1998; Heinz, 1996). Subsequent release of the best candidate species led to significant suppression of whitefly in poinsettia greenhouses (Heinz and Parrella, 1994b) and in caged cotton.

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