Biological Control **17,** 258–266 (2000)
doi:10.1006/bcon.1999.0776, available online at http://www.idealibrary.com on IDEAL®

Field Evaluation of *Amitus bennetti* (Hymenoptera: Platygasteridae), a Parasitoid of *Bemisia argentifolii* (Hemiptera: Aleyrodidae), in Cotton and Bean

Andrea L. Joyce and Thomas S. Bellows[1]

Department of Entomology, University of California, Riverside, California 92521

Received June 10, 1998; accepted August 6, 1999

Field cage experiments were conducted in Riverside, California to quantify the impact of releases of the parasitoid *Amitus bennetti* Viggiani & Evans on mortality of the whitefly *Bemisia argentifolii* Bellows & Perring. Single-row 50-m-long plots were planted with either cotton or bean. Cages were erected over the plants in each row, and adult whiteflies were released into the cages. Approximately 10 days later, adult parasitoids were released. Marked individual whiteflies were scored every 4 days for 6 weeks. Paired life tables were then constructed from census data from release and control cages over a single whitefly generation. Total whitefly mortality in release cages (71% in bean, 61% in cotton) was significantly greater than in control cages (25% in bean, 34% in cotton). The marginal rate for mortality attributable directly to the parasitism was 0.535 in the bean plots and 0.201 in the cotton plots. In addition, other mortality was greater in the release plots, possibly reflecting death of parasitized hosts before larval parasitoids could complete development. Parasitism was the greatest mortality factor in the study.

***Key Words: Bemisia argentifolii; Amitus bennetti;* biological control; natural enemy evaluation; field cage evaluation; life table; percentage parasitism; marginal rates of mortality.**

INTRODUCTION

The silverleaf whitefly, *Bemisia argentifolii* Bellows and Perring, which has been previously referred to as *Bemisia tabaci* (Gennadius) biotype B, is distinguished from *B. tabaci* by size, host range, morphological, and genetic differences (Bellows *et al.,* 1994; Perring, 1995). *B. argentifolii* is distributed throughout the southern United States (Perring *et al.,* 1993) and is a pest of many agricultural and ornamental plants, including cotton, bean, melon, hibiscus, and poinsettia (Gill, 1992; Perring *et al.,* 1992; Summers *et al.,* 1995). Damage to these crops has exceeded hundreds of millions of dollars annually (Perring *et al.,* 1993; Summers *et al.,* 1995). The species is multivoltine and found year round in the Imperial Valley of California (Gruenhagen *et al.,* 1993). Chemical control of this whitefly is commonly practiced, and frequent application of insecticides has played a role in the development of resistance to several insecticides, including organophosphates, pyrethroids, cyclodienes, and carbamates (Prabhaker *et al.,* 1992; Anthony *et al.,* 1995; Dennehy *et al.,* 1996).

B. argentifolii is attacked by several parasitoids native to the Imperial Valley. However, these parasitoids do not exert sufficient control to keep *B. argentifolii* below economic thresholds (Parrella *et al.,* 1992). As part of a larger program studying natural enemies of *B. argentifolii,* we introduced into California the platygasterid parasitoid *Amitus bennetti* Viggiani & Evans. The *A. bennetti* were obtained from Dr. Ru Nguyen at the Division of Plant Industry, Gainesville, Florida. The colony in Florida was started from individuals parasitizing *Bemisia* sp. on *Euphorbia* sp., which were collected by Fred Bennett in Puerto Rico (Viggiani and Evans, 1992). The wasp parasitizes early nymphal instars of *Bemisia* spp.

The objective of this study was to quantify the impact that the parasitoid *A. bennetti* had on *B. argentifolii* populations in field cage conditions in cotton and bean. Several of the methods that exist for evaluating natural enemies include open-field releases, field-cage studies, the use of insecticides to exclude natural enemies, and genetic techniques (Luck *et al.,* 1988; Bellows *et al.,* 1992; Van Driesche and Bellows, 1996). We conducted a field-cage study of this parasitoid on cotton (*Gossypium hirsutum* L.) and bean (*Phaseolus vulgaris* L.) and performed paired life-table analyses to examine the magnitude of causes of mortality for each stage of the whitefly.

MATERIALS AND METHODS

Field and Cage Design

Cotton variety Delta Pine 5241 and bean variety Burpee "Greensleaves" were used as host plants for

[1] To whom correspondence should be addressed. Fax: (909)-787-3086. E-mail: bellows@ucracl.ucr.edu.

1049-9644/00 $35.00

field experiments. Cotton and bean plants were germinated from seed in 1.5-liter pots with UC Soil Mix 2 (Matkin and Chandler, 1957) and maintained in a greenhouse. Plants were watered every other day and fertilized weekly with Miracle Grow (15-30-15). Seedlings were transplanted on May 2, 1995, to a field plot at the Agricultural Operations Facility at the University of California, Riverside. Plants had from six to eight true leaves at the time of transplant, all of which were of suitable age for oviposition by *B. argentifolii.*

The field plot measured 50 m in length × 3 m in width. Three rows on 0.75-m centers were tilled the length of the field. The first and third rows were planted with one of the two host plants. The center row was left fallow to facilitate movement between field cages. Six cages were placed along each row 3 m apart and each cage enclosed 5 plants, for a total of 30 plants per row. Plants were spaced 0.35 m apart inside the cages. A preplant fertilizer (16-16-16) was applied to the soil, and the plants were watered twice weekly by furrow irrigation for approximately 4 h per day. Temperature and percentage humidity were recorded continuously with a hygrothermograph placed in one of the center cages.

Field cages were constructed of 1.25-cm polyvinyl chloride (PVC) pipe, 1.5 × 0.5 × 2.12 m. Each cage was covered with two sheets of white P-17 agryl material, which were secured to the cage with large clips. A 1-cm-diameter 100-cm-long iron reinforcing bar (rebar) was placed 50 cm deep into the soil at each corner of each cage. The PVC pipes at each corner were place over the exposed 50 cm of this pipe. Each cage was further secured with a 5-cm-wide polywebbing strap placed across the top and sides of the cage and fastened into the ground.

Each row was divided for statistical purposes into three blocks with two cages per block to eliminate any effect of distance from the water source. The treatments in each block were control (C) and release (R) cages, which were assigned randomly in each block. Control cages enclosed host plants and whiteflies only, while release cages also included the parasitoid *A. bennetti.*

Whitefly Releases and Tagging of Nymphs

B. argentifolii adults used for experiments were obtained from a colony maintained on cotton at 27°C ± 1°C and 50% RH at the University of California, Riverside. The study design required densities >5 nymphs per leaf to determine the effectiveness of the parasitoid in the release cages; the density of whitefly nymphs on cotton in the field had previously been found to be economically damaging at >5 nymphs per leaf (Naranjo *et al.,* 1996). On 7 June 1995, adult whiteflies were aspirated into glass vials in groups of 100 individuals. The vials were then closed with cotton lint. Vials with adult whiteflies were placed under the foliage in the cages and the cotton lint stopper was removed. One thousand adult whiteflies were released into the cages with cotton plants, and 1500 adult whiteflies were released into each cage with bean plants (more whiteflies were released into the bean cages because the bean plants had approximately 50% more leaves than did the cotton plants). The plants within each cage were covered by a sheet of agryl material for 3 days following whitefly release to confine the whiteflies to the foliage. On 8 June 1995, sufficient numbers of eggs were visible on the undersides of the leaves of both host plants to ensure adequate populations for evaluation. All references to the number of days post-whitefly release refer to days after 7 June.

On 15 and 16 June 1995 (8 and 9 days post-release), settled first-instar nymphs were tagged in all bean cages. First-instar nymphs settled on the cotton leaves by 17 and 18 June (10 and 11 days post-release). Forty settled first-instar nymphs were tagged in each cage. First-instar nymphs were identified with a 20× hand lens and observed for approximately 10 s to ensure that they were settled. A 2-cm-diameter circle was drawn around the nymph, with an additional ink dot marked 0.5 cm to its right side. Usually, two nymphs were tagged per leaf. Maps were drawn showing the location of nymphs on each sample leaf, and nymphs were sequentially numbered on the maps.

Parasitoid Inoculation

Adult parasitoid *A. bennetti* were obtained from a colony maintained at the insectary facility at the University of California, Riverside at 27°C ± 1°C and 50% RH. Our colony of *A. bennetti* was thelytokous (only females have been observed in this work) and solitary (only a single parasitoid pupa developed within any single whitefly host). Newly emerged (0- to 24-h) females were aspirated from an emergence cage into glass vials in groups of 50 on the day of release. On 19 June 1995 (12 days post-release), 300 parasitoids were released into bean release cages and on 21 June (14 days post-release), 250 parasitoids were released into cotton release cages. A larger number of parasitoids were released into bean cages because they appeared to have a higher whitefly density than did the cotton plants. The glass vials containing parasitoids were placed on the soil between the plants, and the cotton stopper was removed from the vials. The plants were covered by agryl material as described for the whitefly releases for 3 days. Plants were inspected the day following the parasitoid release to verify the presence of searching adult parasitoids. The cages in which parasitoids were released are referred to hereafter as release cages. The term "treatments" refers collectively to both the control and the release cages.

Data Collection and Analysis

Beginning on 22 June (15 days post-release) in bean and 24 June 1995 (17 days post-release) in cotton, the developmental stage of all tagged nymphs was recorded twice per week. The numbers of nymphs in each instar that were dead, missing, or parasitized were recorded. The final fate of each nymph was followed until an adult whitefly or parasitoid emerged or the nymph died or disappeared.

Data from all cages of the same treatment of a host plant were combined by totaling the number of whitefly nymphs alive, dead, missing, or parasitized on each sample date. These data were used to construct partial and total population curves for both treatments on the two host plants and to construct life tables. An approximation of developmental time for the whitefly and the parasitoid was also obtained from this information. Analysis of variance was used to determine if there was a significant difference in developmental time of *B. argentifolii* on bean compared to cotton using SAS 6.03 (SAS Institute, 1988). A χ^2 analysis was performed to compare the mortality in each instar in the control cages and release cages for both host plants. Means reported here are given ± standard error of the mean.

Percentage parasitism was determined from data obtained from 28 leaves of both cotton and bean (approximately one from each plant in the study) collected at the end of the life table study. The whitefly nymphs and emerged whiteflies, as well as parasitoid pupae and emerged parasitoids, were counted in a 4-cm^2 area on each leaf. Using this census data, two methods were used to calculate percentage parasitism. The first method calculated percentage parasitism based on evidence of live emergence to the adult stage for both whiteflies and parasitoids. This measure was calculated by dividing the number of emerged parasitoids by the total number of adult whiteflies and parasitoids that had emerged. The second measure calculated percentage parasitism by including emerged and pupal stages of both parasitoids and whiteflies, and was calculated by dividing the sum of parasitoid pupae and emerged parasitoids by the sum of the living and emerged whiteflies together with living parasitoid pupae and emerged parasitoids. Both of these methods can be used in special circumstances to estimate parasitism rates (Van Driesche, 1983; Van Driesche *et al.*, 1991) but the precision of these estimates varies with life histories of the insects involved. These were calculated in this study for the purpose of comparing measures of percentage parasitism with the marginal rates calculated from the life tables.

The life tables list the number of individuals living at the beginning of each stage, l_x, and the number of nymphs dying in each instar, d_x. Mortality in each stage (stage d_x) was separated by causal factor (factor d_x); these factors included dead (dead nymphs remaining on the sample leaves), disappearance (nymphs gone from the sample leaf), or parasitism (nymphs with adult parasitoid emergence holes or mummified by a parasitoid pupae). The final column on the life table is the marginal rate, which is the amount of mortality (expressed as proportion dying) attributable to a factor as if that factor were acting alone rather than contemporaneously with other factors (Elkinton *et al.*, 1992). We used the formulation of marginal value analysis applicable to a parasitoid acting contemporaneously with other factors (such as predation) that remove nymphs from the system (p. 37 of Elkinton *et al.*, 1992).

RESULTS

Partial Population Curves

The whiteflies in bean control cages were all first instars at the beginning of the study (Fig. 1a). The whitefly nymphs were primarily second instars on the next sample date (15 June 1995, 8 days post-whitefly release). The whitefly nymphs molted twice over the period of the next two observations. Adult whiteflies emerged from 1 July through 11 July in the bean cages (24–34 days post-release). The development of nymphs tagged in bean release cages exhibited a similar pattern. Nymphs in cotton control and release cages molted through one instar between each observation date (Fig. 1b). Adult emergence began on 1 July (24 days post-release) and continued until 17 July (40 days post-release) in both control and release cages.

The number of tagged nymphs alive on each sample date in control and release cages is shown for bean in Fig. 1c and for cotton in Fig. 1d. Several of the later sample dates in bean had more whiteflies living in the release cages than in the control cages. Whiteflies developed more rapidly on bean than on cotton. Parasitoids emerged later than whitefly adults in bean (Fig. 1c). The final fate of each nymph was followed until an adult whitefly or parasitoid emerged or the nymph died. The proportion of whiteflies dying was significantly greater in release cages than in control cages (see below).

Developmental Time

Developmental time in the field from egg to adult for *B. argentifolii* averaged 27.2 ± 0.3 days in the bean control cages and 26.4 ± 0.5 days in the bean release cages. Developmental time in bean control cages ranged from 24 to 34 days ($n = 81$) and in bean release cages the range was from 24 to 31 days ($n = 27$). The number of adult whiteflies that emerged on each sample date from tagged nymphs in the bean cages is shown in Fig. 2a. The average developmental time for *B. argentifolii* in cotton was 30.0 ± 0.4 days in control cages and 30.0 ± 0.5 days in release cages. Developmental time in

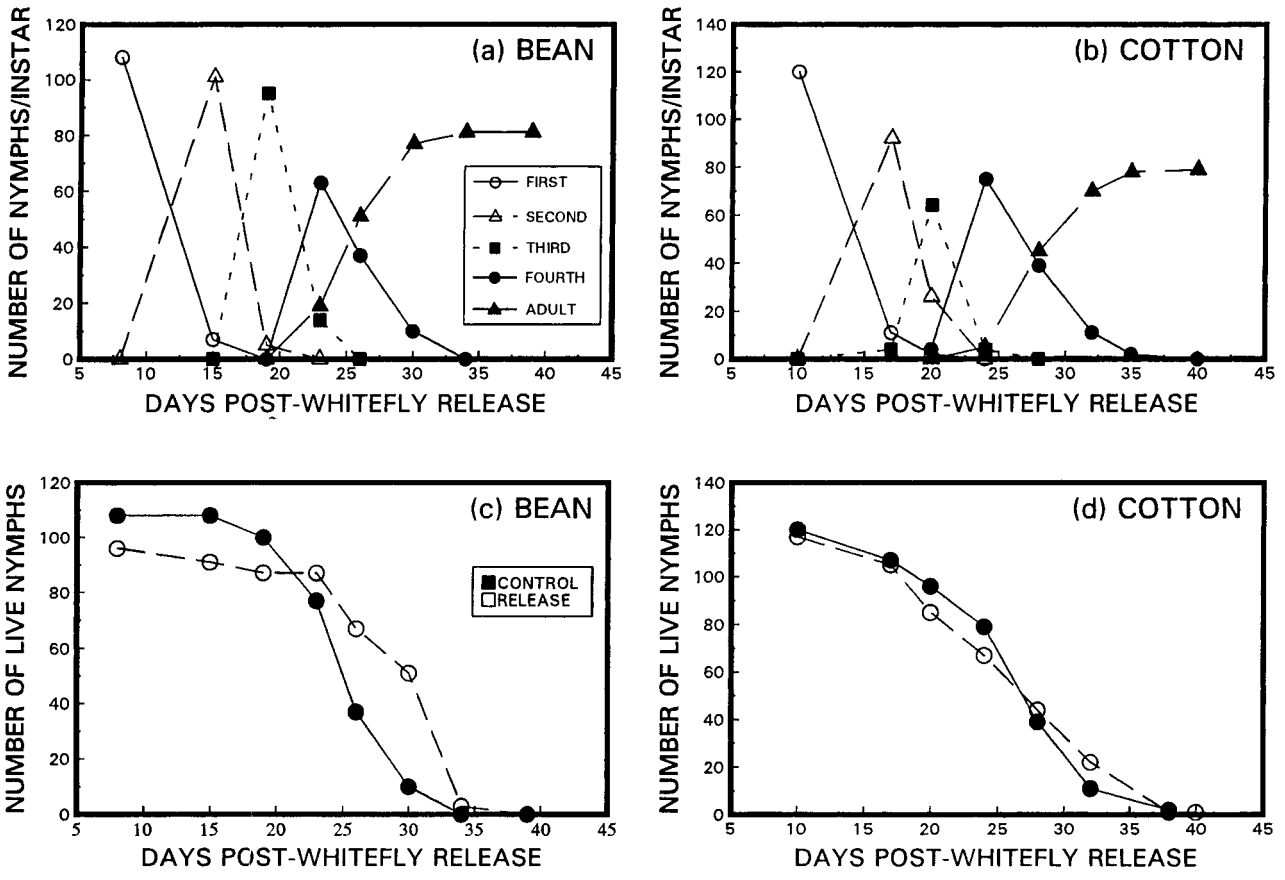

FIG. 1. Partial population curves for tagged *Bemisia argentifolii* nymphs in the bean control (a) and cotton control (b) cages. Total population of tagged *B. argentifolii* nymphs in control and release cages in bean (c) and cotton (d).

the cotton control cages ranged from 24 to 40 days ($n = 79$) and in cotton release cages ranged from 24 to 40 days ($n = 45$). The number of adult whiteflies that emerged on each sample date in cotton cages is shown in Fig. 2b.

No significant difference in developmental time for *B. argentifolii* was found between control and release cages of either bean ($F = 0.04$; $df = 1, 106$; $P > 0.05$) or cotton ($F = 0.64$; $df = 1, 115$; $P > 0.05$). Consequently, the data from control and release cages were pooled for each plant species to compare developmental time on the two plant species. There was a significant difference in the developmental time for *B. argentifolii* between bean (27.0 ± 0.3 days) and cotton (30.0 ± 0.3 days) ($F = 46.94$; $df = 1, 229$; $P < 0.001$).

Developmental time for *A. bennetti*, measured from the day adult parasitoids were released into the cages to the emergence of the progeny adults, averaged 36.1 ± 0.4 days in bean release cages and 35.0 ± 0.7 days in cotton release cages. The range of development time for *A. bennetti* was 32 to 38 days ($n = 26$) in bean and 30 to 36 days ($n = 9$) in cotton. There were no significant differences in developmental time for *A. bennetti* between the two host plants ($F = 1.6$; $df = 1, 33$; $P > 0.05$).

Life Tables

Life tables for control and release cages for bean and cotton are presented in Tables 1 and 2. Dead nymphs appeared flattened or opaque. Nymphs with developing *A. bennetti* developed a black v-shaped area of meconium at the posterior end of the nymph when the parasitoid pupated, and the shape of the whitefly nymph became more convex. These parasitized whiteflies were referred to as "mummies." The parasitoid pupa turned uniformly brown inside its whitefly mummy and gradually became entirely black in color over a few days, at which time it was clearly visible through the whitefly integument. Parasitoid exit holes were close to the anterior end of the whitefly nymph and were circular. The T-shaped exit hole of an adult whitefly on the dorsal surface of exuvia was easily distinguished from circular parasitoid exit holes. Death due to parasitism was assigned to the fourth nymphal instar only, as parasitism due to *A. bennetti* could not be determined prior to this stage.

There was 75% survival of the tagged whitefly nymphs in the bean control cages and 28% survival in the bean release cages (Table 1, Fig. 3). There was 66% survival

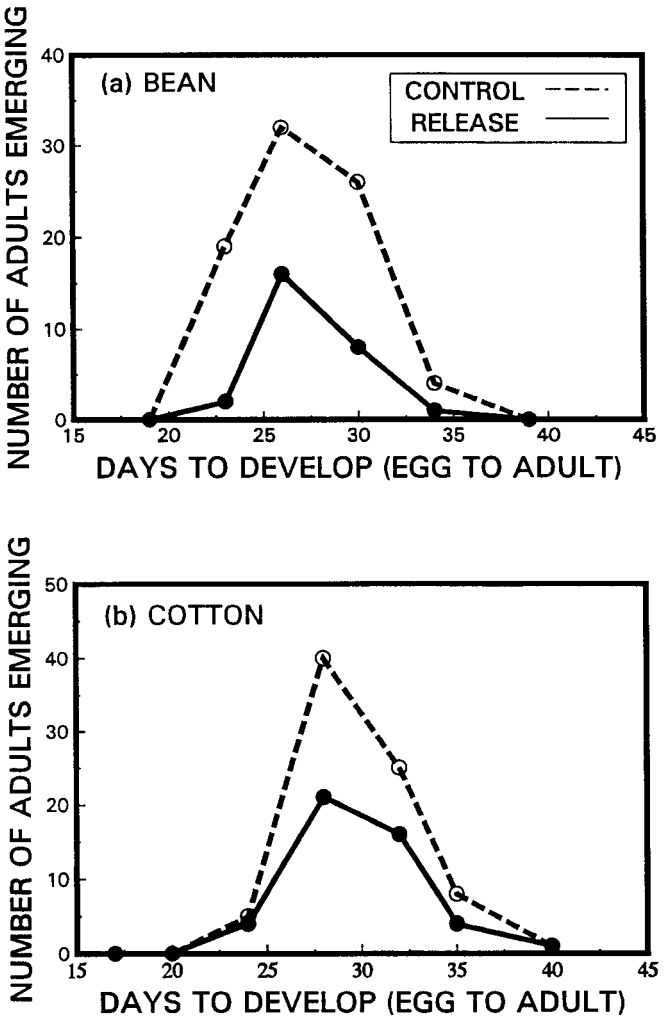

FIG. 2. Developmental time for tagged *Bemisia argentifolii* nymphs in bean (a) and cotton (b).

in the cotton control cages and 38% in the cotton treatment cages (Table 2). Survival in the bean control cages was 168% higher than in the bean release cages, while survival in the cotton control cages was 74% higher than in the cotton release cages. The 95% confidence intervals for the proportion surviving in each treatment for both host plants are shown in Fig. 3. A significantly higher proportion of nymphs survived in the control cages than in the release cages for each host plant (bean, $\chi^2 = 44.8$, $df = 1$, $P < 0.001$; cotton, $\chi^2 = 17.8$, $df = 1$, $P < 0.001$). The proportions surviving in both bean and cotton controls were not significantly different ($\chi^2 = 2.28$, $df = 1$, $P > 0.05$), nor were the proportions surviving in the bean and cotton releases ($\chi^2 = 2.52$, $df = 1$, $P > 0.05$).

A χ^2 analysis of the proportion living and the proportion dying in each whitefly nymphal instar detected no significant difference in mortality between control and release cages in bean for the first ($\chi^2 = 1.75$; $df = 1$; $P > 0.05$), second ($\chi^2 = 0.46$; $df = 1$; $P > 0.05$), and third ($\chi^2 = 1.49$; $df = 1$; $P > 0.05$) nymphal instar. The same analysis in cotton also found no significant difference in the proportion living and dying in the first ($\chi^2 = 0.07$; $df = 1$; $P > 0.05$), second ($\chi^2 = 0.10$; $df = 1$; $P > 0.05$), and third ($\chi^2 = 2.88$; $df = 1$; $P > 0.05$) nymphal instars. There was a significant difference between control and release in the fourth nymphal instar for both bean ($\chi^2 = 10.4$; $df = 1$; $P < 0.05$) and cotton ($\chi^2 = 24.7$; $df = 1$; $P < 0.05$). A χ^2 analysis on fourth nymphal instars comparing the mortality factors death and disappearance (omitting parasitism) showed no significant difference in either bean ($\chi^2 = 0.16$; $df = 1$; $P > 0.05$) or cotton ($\chi^2 = 2.37$; $df = 1$; $P > 0.05$). Parasitism was thus the factor causing the significant difference in mortality in fourth nymphal

TABLE 1

Partial Life Table for *B. argentifolii* in Bean Control and Release Field Cages

		Control				Release			
Stage	Factor	Stage l_x	Stage d_x	Factor d_x	Marginal rate	Stage l_x	Stage d_x	Factor d_x	Marginal rate
First		108	2			96	5		
	Dead			0	0.000			1	0.011
	Missing			2	0.019			4	0.042
Second		106	7			91	4		
	Dead			3	0.029			2	0.022
	Missing			4	0.038			2	0.022
Third		99	4			87	1		
	Dead			3	0.031			1	0.012
	Missing			1	0.010			0	0.000
Fourth		95	14			86	59		
	Parasite			0	0.000			39	0.535
	Dead			12	0.128			16	0.270
	Missing			2	0.023			4	0.076
Adults		81				27			
Total			27				69		

TABLE 2

Partial Life Table for *B. argentifolii* in Cotton Control and Release Field Cages

		Control				Release			
Stage	Factor	Stage l_x	Stage d_x	Factor d_x	Marginal rate	Stage l_x	Stage d_x	Factor d_x	Marginal rate
First		120	16			117	17		
	Dead			1	0.009			0	0.000
	Missing			15	0.126			17	0.145
Second		104	15			100	16		
	Dead			1	0.010			9	0.093
	Missing			14	0.135			7	0.073
Third		89	5			84	11		
	Dead			1	0.012			1	0.013
	Missing			4	0.045			10	0.120
Fourth		84	5			73	28		
	Parasite			0	0.000			13	0.201
	Dead			2	0.024			9	0.144
	Missing			3	0.036			6	0.099
Adults		79				45			
Total			41				72		

instars of the control and release plots in both cotton and bean. The fourth instar had a significantly smaller proportion surviving in release cages than in controls for both bean and cotton.

There was no death recorded in the bean control cages for the first instar (marginal rate is 0). The marginal rate from death for the second to fourth instars ranged from 0.029 to 0.128, with the highest marginal rate from death occurring in the fourth instar. The bean release cages had marginal rates in the first through third instars that ranged from 0.011 to 0.022 (Table 1). The marginal rate from death in the bean release cages in the fourth instar was markedly higher than the marginal rate of death in any stage in both treatments (0.270).

The bean control cages had a narrow range of 0.010–0.038 for the marginal rates due to disappearance (Table 1). The marginal rate of disappearance in bean release cages ranged from 0.0 to 0.076, with the highest rate in the fourth instar. The marginal rate of disappearance in the fourth instar was approximately four times higher in the bean release cages than in the bean control cages (0.076–0.023). Parasitism in the bean release cages had the largest marginal rate of any mortality factor of 0.535 (Fig. 4).

The marginal rates for death in the cotton control cages were similar in the first through third instar, with rates ranging from 0.009 to 0.012. The marginal rate from death in the cotton control was highest in the fourth instar at 0.024. The marginal rate of death in second-instar nymphs in release cages (0.093) was approximately nine times the mortality of death in the control cages (0.010). The marginal rate for death of the fourth nymphal instar in cotton was approximately

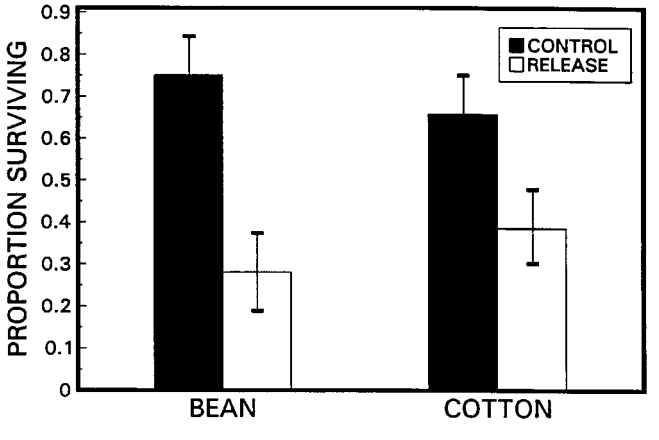

FIG. 3. Proportion (±SE) of *Bemisia argentifolii* nymphs surviving in each treatment.

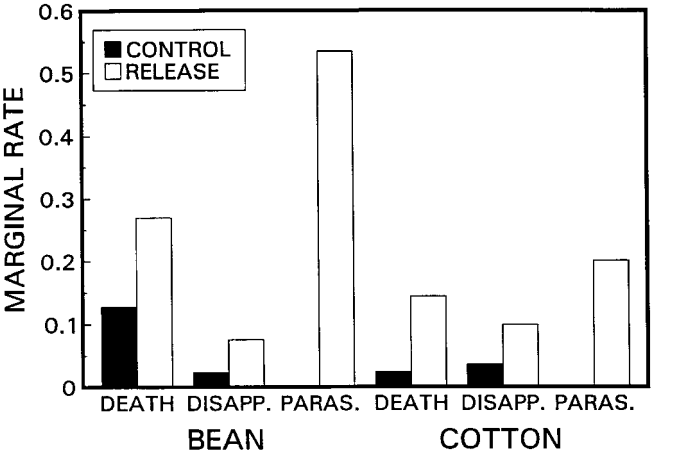

FIG. 4. Marginal rates of mortality from death, disappearance, and parasitism in the fourth-instar nymphs of *Bemisia argentifolii* in the control and release cages in bean and cotton.

seven times greater (0.144) in the release cages than in the control cages (0.024).

The marginal rate of disappearance in the cotton controls ranged from 0.036 to 0.135, with the largest disappearance (0.135) occurring in the first instar and the lowest rate occurring in the fourth instar. The marginal rates from disappearance in the cotton release cages ranged from 0.073 to 0.145. The largest rate of disappearance occurred in the first instar, while the smallest disappearance was in the fourth instar. Parasitism had the largest marginal rate in the fourth instar for the cotton release cages (0.201), higher than any other mortality factor in any stage in either release or control cages (Fig. 4).

Percentage Parasitism

An estimate of percentage parasitism was calculated by dividing the number of nymphs that had parasitoids emerge by the sum of emerged whiteflies and emerged parasitoids. This estimate was 26.1 ± 1.6% in the bean release and 20.5 ± 2.8% in the cotton release cages. Percentage parasitism was estimated by a second method for comparison with the first method. The numbers of live and dead parasitoid pupae and emerged parasitoids were divided by the sum of live, dead, and emerged whiteflies, parasitoid pupae, and emerged parasitoids. The estimate was larger by this method in both bean (31.0 ± 1.4%) and cotton (34.6 ± 2.8%). The actual mortality assignable in the life tables to parasitism in the fourth instar was 53.5% in bean and 20.1% in cotton (Tables 1 and 2).

DISCUSSION

Whitefly nymphs molted between each sample date, every 4 days (Figs. 1a and 1b). Powell and Bellows (1992) found that at 29°C *B. tabaci* took an average of 4.17, 5.17, 2.26, 2.29, and 5.23 days to develop in the egg and four nymphal stadia, respectively. Parasitoids emerged after whitefly emergence on both bean and cotton. The emergence of *A. bennetti* adults coincided with the presence of young-instar nymphs of the F_1 generation. Synchrony of parasitoid emergence with presence of available nymphal hosts has also been reported for *Amitus hesperidum* Silvestri (Dowell, 1979). Populations of *B. argentifolii* in both bean and cotton cages exhibited type 1 survivorship curves with mortality concentrated in the oldest stages of the population (Southwood, 1978).

The developmental time for *B. argentifolii* was significantly longer on cotton than on bean. Insects often have varied developmental times on different host plants. Powell and Bellows (1992) found that *B. tabaci* had a higher developmental rate on cotton than on cucumber at 20–25°C, and the whitefly developed at a lower rate on cotton than on cucumber at 29 and 32°C.

There was no significant difference in the developmental time of *A. bennetti* on *B. argentifolii* when the whitefly was on bean or cotton. Similarly, there was no difference in developmental time of *Eretmocerus eremicus* Rose & Zolnerowich attacking *B. argentifolii* on cotton and sweet potato (Headrick *et al.*, 1996). The mean number of adult progeny of *E. eremicus* was significantly lower on sweet potato (7.5 progeny) than on cotton (25.4 females). A similar trend was observed with the total number of *A. bennetti* that emerged in this field study. A larger number of parasitoids emerged from the marked nymphs on bean (26) than on cotton (9). Headrick *et al.* (1996) suggested that there may be a plant effect on survival of the parasitoid egg, as eggs of *E. eremicus* are oviposited under the host in contact with the leaf suface. The egg of *A. bennetti* is oviposited directly inside the host and not in contact with the leaf. There may be a higher preimaginal mortality of *A. bennetti* in *B. argentifolii* developing on cotton than on bean.

There was a significantly greater total mortality (death, disappearance, and parasitism) of nymphs in the release cages with parasitoids than in control cages for both host plants. The total mortality in bean release cages (72%) was 168% higher than in bean control cages (25%) and in cotton release cages the total mortality (62%) was 82% higher than in cotton control cages (34%). Total mortality did not differ significantly in the release plots for bean and cotton.

There was no significant difference in whitefly nymphal mortality between control and release cages for bean or cotton in the first, second, and third instar. This suggests that the parasitoid had no significant effect on mortality in these stages. Some nymphs may have incurred oviposition attempts but any death was not significantly greater than the general rate of mortality. Host feeding may not play a role in mortality associated with *A. bennetti* in the field, as no host feeding has been observed in laboratory studies on parasitoid behavior for this species (Joyce *et al.*, 1999). Horowitz (1986) found that mortality of *B. tabaci* was highest in the first instar in the field in Israel and suggested that it was due to density-dependent factors and climatic factors, such as variations in temperature and humidity. This illustrates that life table data vary by location and supports the suggestion that life tables for the same insect should be constructed in various locations (Morris, 1957).

Death (i.e., unexplained death in which the dead whitefly nymph remained on the leaf) had a marginal rate of 0.011 in the first instar bean release (Table 1) and 0.000 in the bean control (Table 1). The larger marginal rate for first instars in the bean release cages may be due to the addition of the parasitoid and mortality due to oviposition attempts. The marginal rate for death was highest in the fourth instar in the

bean release (0.270) and bean control (0.128) cages. The marginal rate from death for fourth-instar nymphs in the release cages was approximately twice that of the control. The higher death rate may reflect death from developing parasitoids in the fourth-instar whitefly nymphs. A study of *Encarsia inaron* (Walker) attacking *Siphoninus phillyreae* (Haliday) also found that the marginal rate from death was highest in the two control sites in the fourth instar (0.404, 0.433) and in one of the two release sites (0.541) (Gould *et al.*, 1992). Hoddle and Van Driesche (1996) presented life tables of *B. argentifolii* in greenhouses on poinsettia plants. In their study, the nymphal stages experienced a relatively constant rate of disappearance and death from first to fourth instar. The large natural mortality of *B. argentifolii* in the fourth instar in this study could be from a number of causes, including generalist predators in the families Coccinellidae, Nabidae, Anthocoridae, and Chrysopidae, which were observed regularly in the cages.

Marginal rate for death in the bean control cages increased from the first to the second nymphal instar and then decreased in the third and fourth nymphal instar (Table 1). First-instar whitefly nymphs that died may have fallen off the leaves and thus accounted for the increase in disappearances in the second nymphal instar. In the bean release cages the marginal rate for disappearance decreased from first to second instar and then decreased again in the third nymphal instar (Table 1). The higher marginal rate for disappearance in the bean release for fourth nymphal instars may have been due to developing parasitoids causing the death of fourth-instar nymphs, which may then fall off the leaf. Disappearance can also result from predation.

The bean release cages had a marginal rate of 0.535 from parasitism (Table 1). This was the most significant mortality factor in any fourth nymphal instar in all the bean cages. Gould *et al.* (1992) found marginal rates of parasitism from *E. inaron* on *S. phillyreae* of 0.881 and 0.781 at two release sites, and this was the largest mortality factor in that study. Hoddle and Van Driesche (1996) reported a marginal rate of parasitism of 0.71 by *Encarsia formosa* (Gahan) on *B. argentifolii* in a greenhouse setting. The second largest marginal rate for *B. argentifolii* in the bean release cages was death of fourth nymphal instars (0.270). The highest marginal rate in bean control was 0.128 for death in the fourth nymphal instar (Table 1). Mortality was highest in the fourth instar for both *B. argentifolii* and *S. phillyreae* in sites with or without parasitoids (Gould *et al.*, 1992).

The marginal rate from death (i.e., unexplained death) for whiteflies in the cotton control and release cages had a pattern similar to that in the bean control and release cages. Death in the second instar in the cotton release cages was approximately nine times greater than that in the cotton control cages (Table 2). Although death in the second instar release cages was not significantly higher than death in the control cages, the higher marginal rate from death could reflect death caused by oviposition attempts from released parasitoids. Fourth nymphal instars in release cages evidenced approximately seven times more mortality from unexplained death than did nymphs in the control cages. This may have resulted from developing parasitoids killing nymphs in the fourth nymphal instar in release cages.

The marginal rate from disappearance in cotton was higher in release than in control cages in first, third, and fourth instars (Table 2). Some nymphs may have disappeared or fallen off the leaf after an encounter or oviposition attempt by the parasitoid.

Parasitism had a marginal rate of 0.201 in the cotton release cages (Table 2). This marginal rate was much lower than the 0.535 observed in bean releases and the 0.780 and 0.881 observed by Gould *et al.* (1992) for *S. phillyreae*. The lower marginal rate of parasitism in the cotton cage may reflect differences in the parasitoid searching efficiency on the two host plants or at different densities. *Amitus hesperidum* was thought to be a more effective at controlling *Aleurocanthus woglumi* Ashby at high densities (Dowell, 1979), and a greater search rate may explain the higher marginal rate from parasitism in the bean cages which had significantly greater densities of *B. argentifolii* than that in the cotton cages.

The first method of estimating percentage parasitism gave an estimate of 26% in bean and 21% in cotton. The second method gave higher estimates of 31% in bean and 35% in cotton. The first estimate of percentage parasitism often underestimates the impact of the parasitoid because only hosts that have already died from the parasitoid are counted and developing parasitoids are ignored. The second method of estimating percentage parasitism suggested that there was more parasitism in cotton release cages than in bean releases; however, the marginal rate from parasitism was higher in bean releases than in the cotton release cages. A more precise method of estimating percentage parasitism is to score recruitment by dissecting hosts to determine the proportion of hosts with developing parasitoids (Van Driesche *et al.*, 1991). The most appropriate measure of mortality from parasitism is the marginal rate (Elkinton *et al.*, 1992), which unambiguously quantifies the mortality assignable to a specific cause.

ACKNOWLEDGMENTS

B. Orr assisted in rearing the parasitoid. C. Meisenbacher, A. Cuevas, and C. Breidenbaugh assisted in the field studies. This work was supported in part by the University of California Integrated Pest Management Program and the University of California, Riverside, Experiment Station.

REFERENCES

Anthony, N. M., Brown, J. K., Markham, P. G., and Ffrench-Constant, R. H. 1995. Molecular analysis of cyclodiene resistance-associated mutations among populations of the sweetpotato whitefly *Bemisia tabaci*. *Pestic. Biochem. Physiol.* **51,** 220–228.

Bellows, T. S., Jr., Van Driesche, R. G., and Elkinton, J. S. 1992. Life-table construction and analysis in the evaluation of natural enemies. *Annu. Rev. Entomol.* **37,** 587–614.

Bellows, T. S., Jr., Perring, T. M., Gill, R. J., and Headrick, D. H. 1994. Description of a species of *Bemisia* (Homoptera: Aleyrodidae). *Ann. Entomol. Soc. Am.* **87,** 195–206.

Dennehy, T. J., Ellsworth, P. C., and Nichols, R. L. 1996. "The 1996 Whitefly Resistance Management Program for Arizona Cotton." University of Arizona Cooperative Extension IPM Series No. 8. 16 pp.

Dowell, R. V. 1979. Synchrony and impact of *Amitus hesperidum* (Hymenoptera: Platygasteridae) on its host, *Aleurocanthus woglumi* (Hom: Aleyrodidae) in southern Florida. *Entomophaga* **24,** 221–227.

Elkinton, J. S., Buonaccorsi, J. P., Bellows, T. S. Jr., and Van Driesche, R. G. 1992. Marginal attack rates, *k*-values and density dependence in the analysis of contemporaneous mortality factors. *Res. Popul. Ecol.* **34,** 29–44.

Gill, R. J. 1992. A review of the sweetpotato whitefly in southern California. *Pan-Pac. Entomol.* **68,** 144–152.

Gould, J. R., Bellows, T. S., and Paine, T. D. 1992. Evaluation of biological control of *Siphonius phillyreae* (Haliday) by the parasitoid *Encarsia partenopea* (Walker) using life-table analysis. *Biol. Contr.* **2,** 257–265.

Gruenhagen, N. M., Perring, T. M., Bezark, L. G., Daoud, D. M., and Leigh, T. F. 1993. Silverleaf whitefly present in the San Joaquin Valley. *Calif. Agric.* **47(1),** 4–6.

Headrick, D. H., Bellows, T. S., and Perring, T. M. 1996. Development and reproduction of a population of *Eretmocerus eremicus* (Hymenoptera: Aphelinidae) on *Bemisia argentifolii* (Homoptera: Aleyrodidae). *Environ. Entomol.* **28,** 300–306.

Hoddle, M. S., and Van Driesche, R. 1996. Evaluation of *Encarsia formosa* (Hymenoptera: Aphelinidae) to control *Bemisia argentifolii* (Homoptera: Aleyrodidae) on poinsettia (*Euphorbia pulcherrima*): A lifetable analysis. *Florida Entomol.* **79,** 1–12.

Horowitz, A. R. 1986. Population dynamics of *Bemisia tabaci* (Gennadius), with special emphasis on cotton fields. *Agric. Ecosys. Environ.* **17,** 37–47.

Joyce, A., Bellows, T. S., and Headrick, D. H. 1999. Reproductive biology and search behavior of *Amitus bennetti* (Hymenoptera: Platygasteridae), a parasitoid of *Bemisia argentifolii* (Homoptera: Aleyrodidae). *Environ. Entomol.* **28,** 282–289.

Luck, R. F., Shepard, B. M., and Kenmore, P. E. 1988. Experimental methods for evaluating arthropod natural enemies. *Annu. Rev. Entomol.* **33,** 367–391.

Matkin, O. H., and Chandler, P. A. 1957. The U.C.-type soil mixes. *In* "The U.C. System for Producing Healthy Container-Grown Plants through the Use of Clean Soil, Clean Stock, and Sanitation" (K. F. Baker, Ed.), pp. 68–85. California Agricultural Experiment Station Manual 23, Univ. of California, Berkeley.

Morris, R. F. 1957. The interpretation of mortality data in studies on population dynamics. *Can. Entomol.* **89,** 49–69.

Naranjo, S. E., Chu, C. C., and Henneberry, T. J. 1996. Economic injury levels for *Bemisia tabaci* (Homoptera: Aleyrodidae) in cotton: Impact of crop price, control costs, and efficacy of control. *Crop. Prot.* **15,** 779–788.

Parrella, M. P., Bellows, T. S., Gill, R. J., Brown, J. K., and Heinz, K. M. 1992. Sweetpotato whitefly: Prospects for biological control. *Calif. Agric.* **46(1),** 25–28,

Perring, T. M. 1995. Biological differences of two species of *Bemisia* that contribute to adaptive advantage. *In* "*Bemisia* 1995: Taxonomy, Biology, Damage Control and Management" (D. Gerling and R. T. Mayer, Eds.), pp. 3–16. Intercept, Andover, UK.

Perring, T. M., Cooper, A., and Kazmer, D. J. 1992. Identification of the poinsettia strain of *Bemisia tabaci* (Homoptera: Aleyrodidae) on broccoli by electrophoresis. *J. Econ. Entomol.* **85,** 1278–1284.

Perring, T. M., Farrar, C. A., Bellows, T. S., Cooper, A. D., and Rodriguez, R. J. 1993. Evidence for a new species of whitefly: UCR findings and implications. *Calif. Agric.* **47(1),** 7–8.

Powell, D. A., and Bellows, T. S. Jr. 1992. Preimaginal development and survival of *Bemisia tabaci* on cotton and cucumber. *Environ. Entomol.* **21,** 359–363.

Prabhaker, N., Toscano, N. C., Perring, T. M., Nuessley, G., Kido, K., and Youngman, R. R. 1992. Resistance monitoring of the sweetpotato whitefly (Homoptera: Aleyrodidae) in the Imperial Valley of California. *J. Econ. Entomol.* **85,** 1063–1068.

SAS Institute Inc. 1988. "SAS/STAT user's guide, release 6.03 edition." SAS Institute Inc., Cary, N.C.

Southwood, T. R. E. 1978. "Ecological Methods," 2nd ed. Chapman & Hall, London.

Summers, C. G., Elam, P., and Newton, A. S., Jr. 1995. Colonization of ornamental landscape plants by *Bemisia argentifolii* Bellows and Perring (Homoptera: Aleyrodidae). *Pan-Pac. Entomol.* **71,** 190–198.

Van Driesche, R. G. 1983. The meaning of percent parasitism in studies of insect parasitoids. *Environ. Entomol.* **12,** 1611–1622.

Van Driesche, R. G., and Bellows, T. S. 1996. "Biological Control." Chapman & Hall, New York.

Van Driesche, R. G., Bellows, T. S. Jr., Elkinton, J. S., Gould, J. R., and Ferro, D. N. 1991. Meaning of percentage parasitism revisited: Solutions to the problem of accurately estimating total losses from parasitism. *Environ. Entomol.* **20,** 1–7.

Viggiani, G., and Evans, G. 1992. Descriptions of three new species of *Amitus* Haldeman (Hymenoptera: Platygasteridae), parasitoids of known whiteflies from the New World. *Boll. Lab. Entomol. Agraria "Filippo Silvestri" Portici* **49,** 189–194.