

## Time Delay and Initial Population Density Affect Interactions Between *Encarsia pergandiella* Howard and *Eretmocerus mundus* Mercet (Hymenoptera: Aphelinidae)

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**ABSTRACT** Differences in dispersal abilities between parasitoid species sharing a host may result in asynchronous colonization of host patches and periods of time (delays) when hosts are exploited in the absence of potential competitors. Previous field cage studies showed *Eretmocerus mundus* Mercet and *Encarsia pergandiella* Howard were able to coexist for the duration of a field season when released simultaneously and at the same rate on whitefly-infested cotton plants, and interspecific competition did not influence their ability to suppress their host. The objectives of this study were to investigate the effects of time delay and initial population density on the population dynamics of *En. pergandiella* and *Er. mundus* and their abilities to suppress *Bemisia argentifolii* Bellows and Perring. Field cages enclosing cotton plants were inoculated with whitefly adults and treated by releasing *Er. mundus* and *En. pergandiella* either in sequence (one before the other), at two release rates (1× or 3×), and both in sequence and at two release rates. The sequence of release alone did not affect parasitoid population dynamics. However, when released at two rates, or in sequence and at two rates, the density of *En. pergandiella* was higher at the high rate and when released first. Results suggest that early colonization of host patches is favorable to *En. pergandiella* without a negative impact on host suppression. Results provide insight to explain the observed patterns of establishment and population dynamics of Aphelinid parasitoids assemblages in agroecosystems.

**KEY WORDS** *Encarsia*, *Eretmocerus*, *Bemisia*, interactions, parasitoids

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Ephemeral agroecosystems are characterized by spatial and temporal heterogeneity caused by multiple crop species growing asynchronously through the landscape and over the duration of the growing season. Crops are generally attacked by several herbivore species, and these in turn, by a complex of natural enemy species (Lawton and Strong 1981, Price 1997). Pestiferous insects and their natural enemies tend to move from old crops into new ones as these are harvested and destroyed through agronomic practices and new crops are planted. The effectiveness of natural enemies in the suppression of pest populations in ephemeral agroecosystems depends on their abilities to locate hosts/prey and to quickly respond to variation in their density (Kareiva 1990, van Lenteren et al. 1996). Natural enemy species with better dispersal abilities are able to move into new crops before other species, and this may result in periods of time when host/prey are exploited by individual species in the absence of potential competitors within the natural enemy complex. These periods of time between host exploitation by two or more species of natural enemies are referred in this article as time delays.

*Bemisia argentifolii* Bellows and Perring (Homoptera: Aleyrodidae) is a serious pest of several crops in the southwestern United States causing annual agricultural damage estimated at \$500 million dollars per year (Henneberry et al. 1998). In efforts to prevent *B. argentifolii* outbreaks and enhance the biological control by native natural enemies, 30 species or strains of parasitoids were released in selected areas of the Lower Rio Grande Valley, TX, but evidence only exists of the establishment of three species or strains of *Eretmocerus* (Aphelinidae) (Goolsby et al. 1998, Goolsby et al. 2005). Parasitoids of *B. argentifolii* in most areas of its range include native heteronomous hyperparasitoids (Walter 1983) such as *Encarsia pergandiella* Howard. Heteronomous hyperparasitoids have a unique reproductive strategy; males and females may develop in different host species. The female wasp develops as an obligate primary parasitoid, whereas the male wasp develops as a secondary parasitoid on the immature stages of other Aphelinid species or on females of their own species (Godfray 1994, Hunter and Woolley 2001). *Encarsia pergandiella* was one of the numerically dominant native species of *B. argentifolii* parasitoids in agroecosystems in South Carolina, Texas, Florida, and Central and South America, where surveys were conducted as a part of bio-

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logical control programs against this pest (Riley and Ciomperlik 1997, Bográn et al. 1998, Schuster et al. 1998, Simmons 1998). More recent (2002) field surveys conducted in the Lower Rio Grande Valley of Texas suggest that an exotic species, *Eretmocerus hayati* Zolnerowich and Rose, may have replaced the native *En. pergandiella* as the numerically dominant parasitoid of *Bemisia* whiteflies in the local agroecosystems (Goolsby and Ciomperlik 2005). While predictions from mathematical simulations suggest that heteronomous hyperparasitoids like *En. pergandiella* may hinder the establishment of primary parasitoid species and their effectiveness in reducing host populations (Briggs 1993, Mills and Gutierrez 1996; but see Schreiber et al. 2001), the experimental evidence to support these predictions is rare (Bográn 2000, Bográn et al. 2002, Hunter et al. 2002).

We have conducted a field manipulative study (Bográn et al. 2002) that assessed interspecific interactions between the whitefly parasitoids *Eretmocerus mundus* Mercet, *Encarsia formosa* Gahan, and the heteronomous *En. pergandiella*, and their impact on the suppression of their common host *Bemisia argentifolii*. Using large field cages, parasitoid populations were established by releasing all species combinations of the three parasitoids. Results from these experiments (Bográn et al. 2002) show that the presence of *Er. mundus* reduced the population growth rate of *En. pergandiella* and *En. formosa*. However, the presence of *En. pergandiella* did not affect population growth rates of *Er. mundus*. These results suggest that when released simultaneously, competition and hyperparasitism by heteronomous *En. pergandiella* may not prevent the establishment of other parasitoid species, but cannot explain the observed patterns of species establishment and abundance in agroecosystems where there is likely to be asynchrony in host-patch colonization by different species and where *En. pergandiella* was often a numerically dominant species (Riley and Ciomperlik 1997, Bográn et al. 1998, Schuster et al. 1998, Simmons 1998, but see Goolsby and Ciomperlik 2005).

Differences in dispersal abilities have been documented for parasitoids of *B. argentifolii*. *En. pergandiella* is able to disperse from a point release and locate whitefly-infested plants more quickly than three strains of *Er. mundus*, *En. formosa*, and *Eretmocerus tejanus* Rose and Zolnerowich (Heinz and Parrella 1998). These differences suggest that populations of *B. argentifolii* parasitoids may experience time delays in the exploitation of hosts as resources. Species with better dispersal abilities such as *En. pergandiella* may be able to exploit host patches in the absence of potential competition from other parasitoids and gain a numerical advantage. Predictions from mathematical simulations on the impact of time delays on competitive interactions suggests that the initial population density of competitors may determine which species become numerically dominant (Wagner and Cunningham 1957, Barclay and Van Den Driessche 1975, Wagner 1978, Chesson 1986, Huxel and Hastings 1996). Time delay and the resulting differences in

initial population densities may be a mechanism that enables parasitoids species like *En. pergandiella* to become numerically dominant in agroecosystems.

Few studies have experimentally assessed interspecific competition among parasitoids (Force 1974, Heinz and Nelson 1996, Bográn et al. 2002), and to our knowledge, the impact of time delays on interspecific interactions and parasitoid population dynamics has not been examined experimentally under field conditions. Therefore, the objectives of this study were to investigate the effects of time delay and initial population density on the population dynamics and interspecific interactions of *En. pergandiella* and *Er. mundus*, two parasitoids of *B. argentifolii*, and the effects of these factors on their abilities to suppress their host populations in field cages.

### Materials and Methods

The species of parasitoids included in this study, *En. pergandiella* and *Er. mundus*, are well known (Foltyn and Gerling 1985, Hunter 1989, Gerling et al. 1990, Powell and Bellows 1992, Polaszek et al. 1992, Pedata and Hunter 1996, Liu and Stansly 1996, Schauff et al. 1996, Schuster and Price 1996, Jones and Greenberg 1999). *Er. mundus* is a primary parasitoid; females oviposit underneath second- and third-instar whiteflies (Foltyn and Gerling 1985). *En. pergandiella* is a heteronomous hyperparasitoid (Walter 1983, Godfray 1994). Female wasps develop as primary parasitoids of whitefly, whereas male wasps develop as secondary parasitoids (hyperparasitoids) on the immature stages of other aphelinid parasitoids including its own females. It prefers to lay female eggs in third-instar whitefly but will use a range of host stages from late second to early fourth instars (Liu and Stansly 1996). *En. pergandiella* used in this experiment was mass reared at APHIS-PPQ Plant Protection Center (MPPC), Mission, TX, from material originally collected around Weslaco, TX, in 1998. The *Er. mundus* strain used in the experiments was mass reared at MPPC from material originally collected in Murcia, Spain (identification number M92014; Goolsby et al. 1996). This strain was selected because it had been used in our previous field studies (Bográn et al. 2002) and because at the time it was considered to have good potential as an effective biological control agent (Goolsby et al. 1998, Simmons et al. 2002). *B. argentifolii* used in the experiments were reared on potted Deltapine-50 cotton plants inside a field cage (3.3 m long by 3.3 m wide by 2 m tall) covered by Lumite 52 screening, from material originally collected around campus, Texas A&M University, College Station, TX, in the spring of 1999. Voucher specimens of the two parasitoid species have been deposited in the Texas A&M University Insect Collection.

**Experimental Design.** Populations of the two parasitoids were manipulated using large field cages (3.3 m long, by 3.3 m wide by 2 m tall) covered by Lumite 52 screening material. The cages permitted the establishment of uniform whitefly host populations and the exclusion of other herbivores and parasitoids

**Table 1.** Parasitoid release regimens for field cage experiments assessing the effect of time delay and initial population density on interspecific competition between the parasitoids *Er. mundus* and *En. pergandiella*

Treatment no. (designation)	Week 1	Week 3
1 (Em–Ep)	Em	Ep
2 (Ep–Em)	Ep	Em
3 (Em+3Ep)	Em+3Ep	No release
4 (3Em+Ep)	3Em+Ep	No release
5 (Em–3Ep)	Em	3Ep
6 (3Em–Ep)	3Em	Ep
7 (Ep–3Em)	Ep	3Em
8 (3Ep–Em)	3Ep	Em
9 (Control)	No release	No release

All release regimens were replicated four times ( $n = 4$ ).

<sup>a</sup> All treatment and control cages were inoculated with whitefly by releasing two adults per plant per week for 2 wk before parasitoid releases. Two parasitoid releases were made in week 1 (days 1 and 3) and two in week 3 (days 12 and 14).

Em, *Er. mundus*; Ep, *En. pergandiella*.

to create homogeneous experimental units. Experiments were conducted on 5 ha of unsprayed cotton (Deltapine-50) at the Biological Control Laboratory field research area, near the campus at Texas A&M University in the summer of 1999. Cages enclosing 100 cotton plants were inoculated with whitefly by releasing adults at a rate of two per plant per week for 2 consecutive wk. Whitefly inoculations started when cotton plants reached three main nodes. Because the outcome of interspecific competition may be influenced by the magnitude of the time delay and the initial population density of competitors (Wagernsky and Cunningham 1957, Barclay and Van Den Driessche 1975, Wagernsky 1978, Chesson 1986, Huxel and Hastings 1996), treatments were designed to test the effects of both a 2-wk time delay and a three-fold difference in initial population density. *Er. mundus* and *En. pergandiella* were released into the field cages under three release regimens: (1) in sequence and under a 2-wk time delay (Em–Ep and Ep–Em); (2) simultaneously and at two release rates (3Em+Ep and Em+3Ep); and (3) in sequence (under a 2-wk time delay) and at two release rates (3Em–Ep, Ep–3Em, Em–3Ep, and Em–3Ep). In addition, a no parasitoid release (control) treatment was included to test for the effects of parasitoid releases on host population suppression (Table 1). Parasitoid release rates used were one female (1×) or three females (3×) per plant per release. A total of four parasitoid releases were made, two in week 1 and two in week 3 (see Table 1). Treatments were assigned to experimental units (cages) under a completely randomized block design with four repetitions (9 treatments × 4 repetitions = 36 cages).

Parasitoid releases started 2 wk after the first whitefly inoculation to ensure that suitable stages of the host were readily available for parasitoid population establishment. The length of the time delay used was 12–14 d. The magnitude of the time delay was selected based on the reproductive biology of *Er. mundus* and *En. pergandiella* (Foltyn and Gerling

1985, Hunter 1989, Pedata and Hunter 1996, Liu and Stansly 1996, Schauff et al. 1996), previous observations on parasitoid populations colonizing hosts in field cages (Bográn et al. 2002), and to increase our chances to detect a possible time-delay effect. The chosen time delay represents the approximate time needed for *Er. mundus* to parasitize their host and reach the third-instar and prepupal stages, when it is most susceptible to hyperparasitism by *En. pergandiella* (Bográn 2000, Bográn and Heinz 2002).

Female whitefly generally deposit eggs on young leaves, and as the plant grows, the distribution of whitefly and parasitoid life stages becomes stratified along each growing shoot (Naranjo and Flint 1994). Therefore, vertically stratified samples were taken by collecting the main stem leaves of three arbitrarily chosen plants per cage. Sampling was done every 14 d for 8 wk (four sampling dates) starting 2 wk after the last parasitoid release. Leaves were taken to the laboratory in plastic bags, and counts were performed on each leaf with the aid of a dissecting microscope. Census included whitefly immatures by stage and immature parasitoids by species. *Eretmocerus* and *Encarsia* immatures are easily distinguished when they are first visible through the whitefly cuticle. Larval *Eretmocerus* are almost spherical and can first be seen as a cloudy area in the center of the whitefly nymph, whereas *Encarsia* may first be recognized by the appearance of the hymenoptera-like larval form. Prepupal and pupal *Eretmocerus* can be easily distinguished from *Encarsia* of the same stage because they do not deposit meconial pellets. When densities per leaf exceeded 100 for any of the census categories, subsamples were made by censusing four leaf discs (1 cm<sup>2</sup> each) per leaf. Leaf disks were taken from the basal part of the leaf and from each of the four areas of the leaf separated by the main veins (see Naranjo and Flint 1994). At the conclusion of each census, leaf areas were determined with the aid of an area machine (model CI-203; CID, Vancouver, WA), and insect densities were standardized to number per square centimeter of abaxial leaf surface to facilitate statistical analyses and graphical representation of the results.

**Statistical Analyses: Parasitoids.** The impact of time delay and initial population density on the outcome of competitive interactions between *Er. mundus* and *En. pergandiella* was assessed by comparing population densities of each species between the different release conditions. Data on parasitoid abundance over time were used to test three hypotheses: (1) a 2-wk time delay does not influence population density of *Er. mundus* and *En. pergandiella* in field cages, (2) a three-fold difference in release rate does not cause a significant difference in population density for *Er. mundus* and *En. pergandiella*; and (3) the combination of a 2-wk time delay and a three-fold difference in release rate does not differentially influence population density of *Er. mundus* and *En. pergandiella*. To test the first hypothesis, we compared population density of each parasitoid species between treatment Em–Ep and treatment Ep–Em (Table 1). A significant difference would indicate an influence of the order in

which parasitoids are released (under a 2-wk delay) on parasitoid population density.

To test the second hypothesis, we compared population density of each parasitoid species between treatment 3Em+Ep and treatment Em+3Ep (Table 1). A significant difference in parasitoid population density favoring the high release rate would indicate that the initial release rate is an important factor determining parasitoid population dynamics of *Er. mundus* and *En. pergandiella*. Alternatively, lack of a significant difference or a difference favoring the lower release rate would indicate that initial release rate does not determine population density of *Er. mundus* and *En. pergandiella* and would suggest that interspecific interactions are more important than the initial release rate in determining parasitoid population density in field cages.

To test the third hypothesis, we compared parasitoid population density for each parasitoid species between treatments Em-3Ep, 3Em-Ep, Ep-3Em, and 3Ep-Em (Table 1). Significant differences between treatments in which parasitoids were released in a different sequence but at the same release rate (Em-3Ep versus 3Ep-Em and 3Em-Ep versus Ep-3Em) would indicate that the influence of the order in which parasitoids are released on parasitoid population density is independent of the initial release rate of competitors. Significant differences between treatments in which parasitoids were released in the same sequence but at different release rates (Em-3Ep versus 3Em-Ep and Ep-3Em versus 3Ep-Em) would indicate that the initial release rate may determine parasitoid population density even when parasitoids are released under a 2-wk delay. A significant difference in population density between treatments in which parasitoids were released in a different sequence and at two release rates (Em-3Ep versus Ep-3Em) favoring the higher release rate would indicate that the influence of the initial release rate on parasitoid population density is independent of the order in which parasitoids are released. Alternatively a significant difference favoring the lower release rate would indicate that the order in which parasitoids are released is more important in determining parasitoid population density than the initial release rates.

Because each cage was isolated from others, individually treated, and sampled repeatedly through the study, a repeated-measures analysis of variance (ANOVA) was conducted to detect significant differences among treatment means (von Ende 1993). Pre-planned contrasts were used to test the three hypotheses and to separate treatment means (see Table 1). Because both parasitoid species are relatively short-lived (<17 d between generations) and populations were sampled every 2 wk, analyses involving parasitoids was performed on pooled data across all immature stages. Similarly, analyses involving whitefly was performed on pooled data across all whitefly developmental stages.

**Statistical Analyses: Whitefly.** The ability of parasitoid releases to suppress their host populations was assessed by comparing *B. argentifolii* population den-

sities in the control (no parasitoids released) to those in the parasitoid release treatments. A lower *B. argentifolii* population density in parasitoid release cages compared with the control cages would indicate that parasitoid releases were capable of host population suppression. The effect of time delay on the population dynamics of *B. argentifolii* was assessed by comparing whitefly density in the control treatment with that in treatments where parasitoids were released in sequence and at the same release rate (Table 1). The effect of initial population density on host population suppression was assessed by comparing *B. argentifolii* density in the control treatment to that in release treatments in which the parasitoids were released simultaneously but at different release rates (Table 1). The combined effects of time delay and initial population density on host population suppression were assessed by comparing *B. argentifolii* density between the control treatment and release treatments in which the parasitoids were released in sequence and at different release rates (Table 1). Differences among parasitoid release treatments in the population density of *B. argentifolii* would indicate an impact of the release condition on the levels of host suppression by the two parasitoids.

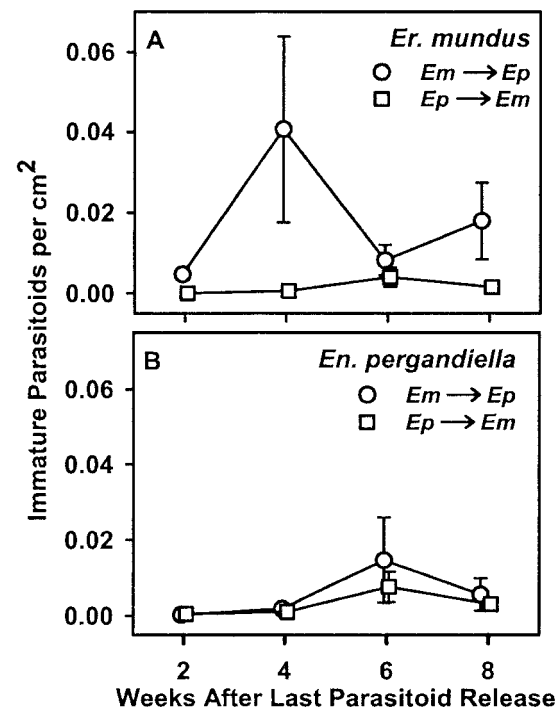


Fig. 1. Parasitoid population density over time for releases under a 2-wk delay and at the rate of one female per plant per release (in all cases, parasitoid releases ended on week 0). (A) *Eretmocerus mundus* (Em). (B) *Encarsia pergandiella* (Ep). Circles, Em released before Ep; squares, the opposite.

Results

*Bemisia argentifolii* was established in all cages, and the population density of all immature stages reached two to four nymphs per leaf ( $114 \pm 9 \text{ cm}^2$ ,  $n = 36$ ) 4 d before parasitoid releases started. No significant differences among treatments were found in the total number of immature whiteflies present in cages before parasitoid releases ( $F = 0.63$ ;  $df = 8,24$ ;  $P = 0.75$ ). The parasitoid population density for each species, in cages where parasitoid releases were made under a 2-wk time delay, and at the same release rate appears in Fig. 1. The population density of both *Er. mundus* and *En. pergandiella* was similar between treatment Em–Ep and treatment Ep–Em. Only at 4 wk after the last parasitoid release was a significant difference observed in the population density of *Er. mundus*. On this date, the average density of *Er. mundus* was higher in treatment Em–Ep than in treatment Ep–Em (univariate ANOVA contrast,  $F = 5.41$ ;  $df = 1,24$ ;  $P = 0.03$ ; Fig. 1). However, this difference was not large enough to cause a significant effect when all sampling dates were pooled (repeated-measures ANOVA contrast:  $F = 0.95$ ;  $df = 1,24$ ;  $P = 0.34$ ). In contrast, *En. pergandiella* densities were always similar ( $P > 0.5$ ) between treatment Em–Ep and treatment Ep–Em (Fig. 1).

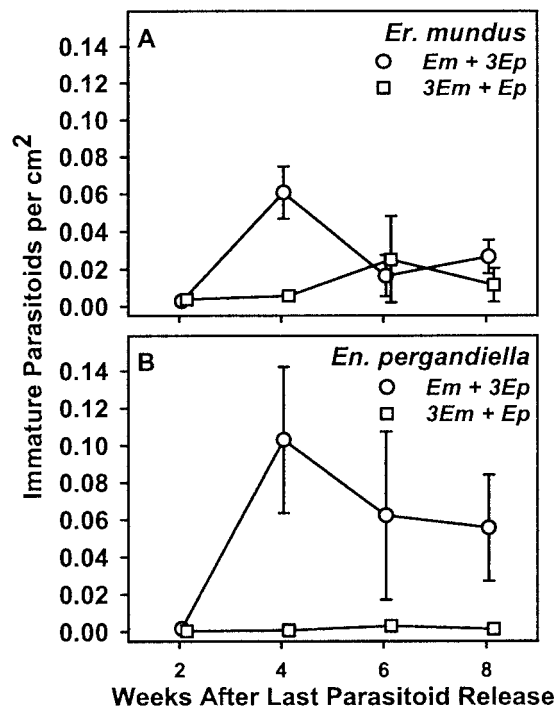


Fig. 2. Parasitoid population density over time for simultaneous releases at the rate of one (1×) or three (3×) females per plant per release (in all cases, parasitoid releases ended on week 0). (A) *Eretmocerus mundus* (Em). (B) *Encarsia pergandiella* (Ep). Circles, releases of Em at 1× and Ep at 3×; squares, releases of Em at 3× and Ep at 1×.

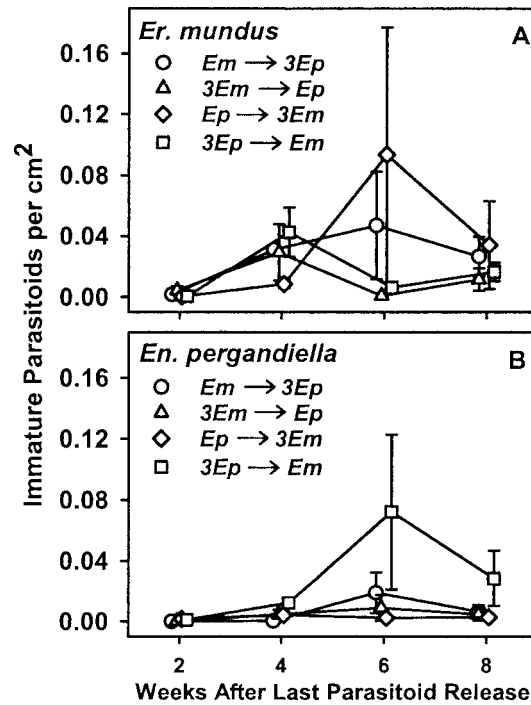


Fig. 3. Parasitoid population density over time for releases under a 2-wk delay and at the rate of one (1×) or three (3×) females per plant per release (in all cases, parasitoid releases ended on week 0). (A) *Eretmocerus mundus* (Em). (B) *Encarsia pergandiella* (Ep). Circles, 1×Em released before 3×Ep; triangles, 3×Em released before 1×Ep; diamonds, 1×Ep released before 3×Em; squares, 3×Ep released before 1×Em.

The parasitoid population density for each species in cages where parasitoid releases were made simultaneously and at a different release rate appears in Fig. 2. Parasitoid population density was similar for *Er. mundus*, but significantly different for *En. pergandiella* between treatment Em+3Ep and treatment 3Em+Ep. A significant difference was observed on the population density of *Er. mundus* only at 4 wk after the last parasitoid release (univariate contrast,  $F = 15.1$ ;  $df = 1,24$ ;  $P < 0.001$ ; Fig. 2). However, this difference was not large enough to cause a significant effect when all sampling dates were pooled (repeated-measures ANOVA contrast:  $F = 1.1$ ;  $df = 1,24$ ;  $P = 0.30$ ). *En. pergandiella* densities were significantly higher in treatment Em+3Ep than in treatment 3Em+Ep at 4 (univariate ANOVA contrast:  $F = 23.0$ ;  $df = 1,24$ ;  $P < 0.001$ ) and 8 wk (univariate ANOVA contrast:  $F = 8.3$ ;  $df = 1,24$ ;  $P < 0.01$ ) after the last parasitoid release (Fig. 2). This difference was also significant when the population density of *En. pergandiella* was pooled across all sampling dates (repeated-measures ANOVA contrast:  $F = 20.1$ ;  $df = 1,24$ ;  $P < 0.001$ ). The parasitoid population density for each species in cages where releases were made under a 2-wk time delay and at a different release rate appears in Fig. 3. No significant

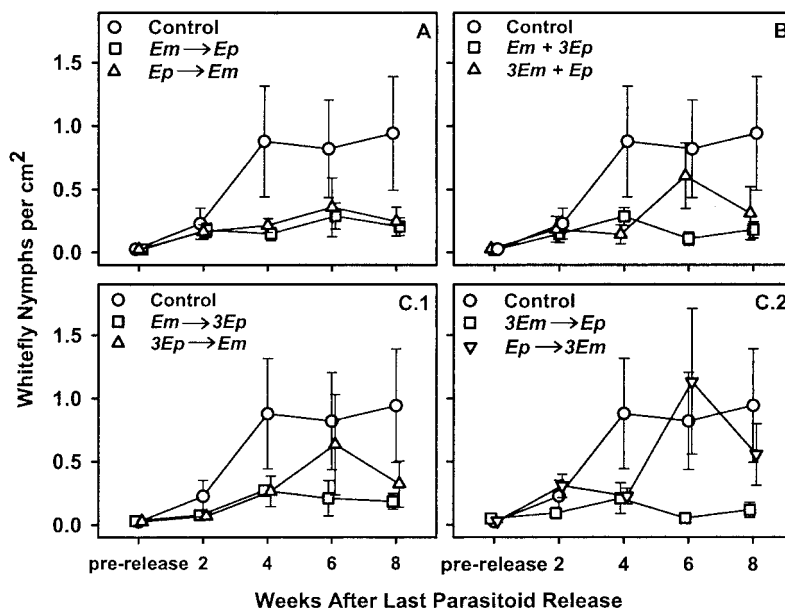


Fig. 4. *Bemisia argentifolii* population density over time in each parasitoid release treatment and the control. (A) Parasitoid released under a 2-wk delay. (B). Parasitoids released simultaneously and at the rate one (1 $\times$ ) or three (3 $\times$ ) females per plant per release. (C) Parasitoids released under a 2-wk delay and at the rate one (1 $\times$ ) or three (3 $\times$ ) females per plant per release. Circles, control treatment.

differences between treatments were found in the density of *Er. mundus* for any of the paired treatment comparisons ( $P > 0.2$ ). In contrast, the population density of *En. pergandiella* across sampling dates was higher in treatment 3Ep–Em than on treatment Em–3Ep (repeated-measures ANOVA contrast:  $F = 4.8$ ;  $df = 1,24$ ;  $P = 0.04$ ) and smaller in treatment Ep–3Em than in treatment 3Ep–Em (repeated-measures ANOVA contrast:  $F = 6.5$ ;  $df = 1,24$ ;  $P = 0.02$ ; Fig. 3). However, no significant difference was found in the population density of *En. pergandiella* between treatment Em–3Ep and treatment 3Em–Ep (repeated-measures ANOVA contrast:  $F = 0.3$ ;  $df = 1,24$ ;  $P = 0.86$ ) or between treatment Em–3Ep and treatment Ep–3Em (repeated-measures ANOVA contrast:  $F = 0.1$ ;  $df = 1,24$ ;  $P = 0.72$ ).

The average number of immature *B. argentifolii* in each parasitoid release treatment and the no-parasitoid release control appears in Fig. 4. A significant treatment effect was found on the density of *B. argentifolii* nymphs ( $F = 3.6$ ;  $df = 8,27$ ;  $P = 0.006$ ), but the magnitude of the difference among treatments varied with time ( $F = 1.71$ ;  $df = 24,81$ ;  $P = 0.049$ ). The average number of *B. argentifolii* nymphs was higher in the control treatment than in parasitoid release treatments (repeated-measures ANOVA contrast:  $F = 24.2$ ;  $df = 1,27$ ;  $P < 0.001$ ; Fig. 4). The population density of *B. argentifolii* was similar between cages in which parasitoids were released under a 2-wk time delay and at the same release rate (treatment Em–Ep and treatment Ep–Em;  $P > 0.9$ ) and between cages in which parasitoids were released simultaneously and at a different release rate (treatment 3Em+Ep and treat-

ment Em+3Ep;  $P > 0.4$ ). In addition, no significant differences were found in the density of *B. argentifolii* between treatments in which parasitoids were released under a 2-wk time delay and at a different release rate (treatments Em–3Ep, 3Ep–Em, 3Em–Ep, and Ep–3Em;  $P > 0.1$ ). Only at 6 wk after the last parasitoid release was a significant difference observed in *B. argentifolii* density among parasitoid release treatments. On this date, the density of *B. argentifolii* was higher in treatment Ep–3Em than on 3Em–Ep ( $F = 3.6$ ;  $df = 8,27$ ;  $P = 0.006$ ). However, no significant differences were found on this date between the control and any of the parasitoid release treatments (Fig. 4).

## Discussion

In this study, the population densities of *Er. mundus* and *En. pergandiella* were compared between cages in which these parasitoids were released in sequence and at two release rates to assess the influence of a time delay and a three-fold difference in initial population density on the outcome of competitive interactions among the two parasitoids. A 2-wk time delay between the release of *Er. mundus* and *En. pergandiella* did not have an impact on the dynamics of these two species when the parasitoids were released at the same release rate. However, the release rate significantly influenced the population dynamics of *Er. mundus* and *En. pergandiella* when the parasitoids were released simultaneously or under a 2-wk delay.

The lack of a significant difference in the population density of *Er. mundus* between treatments in

which the parasitoids were released simultaneously and at two release rates suggests that interactions between *Er. mundus* and *En. pergandiella* may negatively influence *Er. mundus* populations. The sequence in which the two species were released did not alter this outcome, because *Er. mundus* population density was always similar between cages in which the two species were released at two rates, regardless of the release sequence. Hyperparasitism by *En. pergandiella* may have contributed to this outcome. Differences in the window of vulnerability to hyperparasitism by *En. pergandiella* between secondary host species have been observed in the laboratory (Hunter and Kelly 1998). The longer developmental time of *Er. mundus* compared with *En. pergandiella* may have increased its susceptibility to hyperparasitism. In addition, the frequency of hyperparasitism by heteronomous hyperparasitoids may be a function of overall host availability and the relative abundance of primary and secondary hosts species (Hunter and Godfray 1995). Although we were unable to detect and test for differences in hyperparasitism between cages, hyperparasitism intensity may have shifted to the more frequently encountered host contributing to the observed pattern. Laboratory observations on host preference by *En. pergandiella* suggest that this species did not prefer *Er. mundus* over its own females or over *B. argentifolii* when their abundances were similar (Bográn and Heinz 2002).

*Encarsia pergandiella* population density was not affected by *Er. mundus* when the two species were released simultaneously and at two release rates. As expected, *En. pergandiella* population density was higher when it was released at the higher release rate. However, the sequence in which the two species were released did alter this outcome. *En. pergandiella* population density was similar between cages in which the parasitoids were released at two release rates and *En. pergandiella* was released after *Er. mundus*. This suggests that interactions between *Er. mundus* and *En. pergandiella* negatively affected *En. pergandiella* populations only when it was released after *Er. mundus*. This may have been caused by the ability of *Er. mundus* to attack earlier host stages than *En. pergandiella* and is consistent with earlier results (Bográn et al. 2002) where we found that the presence of *Er. mundus* reduced population growth rates of *En. pergandiella*. These results suggest that, under field conditions, the early colonization of host patches may be favorable to *En. pergandiella* but may not favor *Er. mundus*.

In a laboratory experiment, Heinz and Parrella (1998) found that *En. pergandiella* located whitefly-infested plants more quickly than *Er. mundus*, *En. formosa*, *Er. tejanus*, and two other *Er. mundus* strains. In this study, *En. pergandiella* populations were larger when *En. pergandiella* was released before *Er. mundus*. These results suggest that, under natural conditions, *En. pergandiella* may be favored by getting to the host resource before other species. Surveys of *Bemisia* parasitoids in the Lower Rio Grande Valley, TX, and in coastal South Carolina indicated that *En. pergandiella* was one of the numerically dominant parasitoid

species in local agroecosystems (Riley and Ciomperlik 1997, Simmons 1998). Superior dispersal abilities of parasitoids like *En. pergandiella* causing a time delay in colonization by potential competitors may help explain their numerical dominance in agroecosystems.

Comparisons of the population density of *B. argentifolii* between treatments suggest that any interaction between *Er. mundus* and *En. pergandiella* released under a 2-wk time delay and at two initial population densities did not negatively influence whitefly host suppression. All release treatments were similarly capable of reducing whitefly population densities relative to the densities in the control. Whitefly densities in the control cages were on average 5–10 times larger than in cages receiving parasitoid releases. This suggests that time delays and differences in initial population densities caused by dissimilar dispersal abilities of aphelinid parasitoids may not prevent successful host suppression by the parasitoid assemblage.

Results from this study and our previous study (Bográn et al. 2002) suggest that the low establishment rates of introduced species of parasitoids released against *B. argentifolii* is not likely caused by interspecific competition within the parasitoid assemblage or to hyperparasitism by the heteronomous *En. pergandiella*. In all cases, and under all tested release conditions, parasitoid populations were established and persisted through the experiments, even under contrasting initial release rates. The lack of establishment of many exotic parasitoid species released in the Lower Rio Grande Valley of Texas may have been affected by such factors as whitefly host-race specificity, tritrophic interactions with the local host plant species (wild and cultivated), and poor climatic match between areas of origin and areas of release (Goolsby et al. 2005). Interspecific competition among aphelinid parasitoids occurring during a single growing season does not seem important in determining which species are present within the aphelinid parasitoid assemblage. In addition, interspecific competition among aphelinid parasitoids occurring during a single growing season does not seem to hinder host population suppression.

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