

## BIOLOGICAL CONTROL

# Augmentation of the Egg Parasitoid *Anaphes iole* (Hymenoptera: Mymaridae) for *Lygus hesperus* (Heteroptera: Miridae) Management in Strawberries

ANDREW P. NORTON<sup>1</sup> AND STEPHEN C. WELTER

Department of Environmental Science, Policy, and Management, University of California, Berkeley, Berkeley, CA 94720

Environ. Entomol. 25(6): 1406–1414 (1996)

**ABSTRACT** The impact of repeated releases of *Anaphes iole* (Girault) on the development of *Lygus hesperus* Knight populations and fruit damage in commercial strawberry fields was evaluated. Following the release of 37,000 parasitoids per hectare, 50% of *L. hesperus* eggs were parasitized. Parasitism levels declined rapidly; after 96 h, parasitism levels had declined to an average of only 3.5% in these plots. A release rate of 12,300 parasitoids per hectare produced parasitism levels of 6.3 and 7.0% 48 and 96 h after release, respectively. The high release rate of the parasitoids resulted in a 43% reduction in the number of *L. hesperus* nymphs and a 22% reduction in the amount of fruit damage. The low release rate responded in a comparable fashion, with nymph and damage levels 19 and 14% lower than control plots, respectively. The effect of the parasitoid releases on *L. hesperus* populations increased through time. On average, there was a proportionally greater reduction in nymph densities in the higher release rate plots during the latter half of the season. In all the plots, there was a significant relationship between the number of *L. hesperus* nymphs found in the plot and the amount of fruit damage. The significance of these results to management of *L. hesperus* in strawberries is discussed.

**KEY WORDS** *Lygus hesperus*, *Anaphes iole*, biological control, augmentation, strawberry, *fragaria*

*Lygus* BUGS (*Lygus hesperus* Knight, *L. lineolaris* Palisot de Beauvois, and *L. elisus* Van Duzee) are serious pests of a wide variety of crops, including cotton, *Gossypium hirsutum* L (Leigh and Wynholds, 1988); seed alfalfa *Medicago sativa* L, (Sorenson 1936); oil seed rape (Butts and Lamb 1991); and strawberries, *Fragaria x annassa* Duchesne (Allen and Gaede 1963, Schaefer 1966). *L. hesperus* is the predominant pest species in the western United States and *L. lineolaris* is the predominant pest in the east, although *L. lineolaris* is also found in the west. *Lygus* spp. cause damage by feeding on the developing fruit and seeds of plant hosts. When *Lygus* spp. damage the marketable portion of the crop, feeding results in direct yield loss, which may produce low damage thresholds.

The ecology of *Lygus* spp. is similar across plant hosts and species. *Lygus* spp. overwinter as adults and begin oviposition in early spring. Depending on temperature conditions, *Lygus* spp. may go through 1–5 generations per year (Strong et al. 1970, Gutierrez et al. 1977, Schwartz and Footitt 1992). *L. hesperus* and *lineolaris* are both broadly

polyphagous (Stitt 1949, Snodgrass et al. 1984, Young 1986). Adult *Lygus* spp. move from one host plant to the next as each plant begins to flower (Graham et al. 1986, Fleischer and Gaylor 1987, Stewart and Gaylor 1994). *Lygus* spp. are relatively long-lived and oviposition occurs throughout the life span of the adult.

In the central coastal area of California, *L. hesperus* is the key pest of strawberries. Feeding by *L. hesperus* nymphs on the achenes of developing fruits results in deformed or “cat-faced” fruit. Because the majority of fruit is grown for fresh market sale and deformed fruit is not acceptable to consumers, *L. hesperus* nymphs are capable of inflicting substantial yield losses. Current control strategies for *L. hesperus* rely on the regular application of broad spectrum insecticides (University of California IPM Project 1994). Application of insecticides to control *L. hesperus* often results in a reduction in natural enemy populations, resulting in outbreaks of other pests such as the twospotted spider mite, *Tetranychus urticae* Koch. Thus, chemical control of *L. hesperus* may result in increased applications of acaricides to control mite outbreaks. Increasing the number of acaricide applications accelerates the rate of resistance development by spider mites to the few compounds

<sup>1</sup>Current address: Department of Entomology, New York State Agricultural Experiment Station, Cornell University, Geneva, NY 14456.

that remain effective (Zalom et al. 1990, Parrella et al. 1992, University of California 1994). In addition, many strawberry growers in this region use releases of the predatory mite *Phytoseiulus persimilis* Athias-Henriot for an integrated spider mite management program. Chemical control of *L. hesperus* interferes with this mite biological control program, thus making management decisions more complex and less reliable. An alternative control strategy for *L. hesperus* that does not result in the disruption of existing biological controls could have broad reaching benefits for pest management in strawberries. An effective biological control strategy, either as an alternative or in addition to existing management practices, could greatly reduce the direct and indirect losses from this pest.

There have been many research efforts on the biological control of *Lygus* species (reviewed by Hedlund and Graham 1987). Much of this research concentrates on the release and establishment of exotic natural enemies of *Lygus* spp. However, there have been relatively few successes from these efforts (though see Day et al. 1990). There are many hypotheses for the apparent lack of success of classical biological control of *Lygus* spp., and it is likely that the broad host range of these insects coupled with their rapid dispersal to and colonization of a sequence of hosts may limit the effectiveness of many natural enemies in agricultural situations (Norton et al. 1992). Rapid colonization by *Lygus* adults, coupled with the low damage thresholds for *Lygus* spp. in many crops, makes it less likely that enough natural enemies will be present in the crop early enough to prevent populations from reaching damaging levels.

Augmentative biological control is the periodic release of natural enemy populations for the control or reduction of pest species. If releases of a biological control agent are timed to coincide with the appearance of *Lygus* populations in the host crop, successful biological control may be achieved early enough in the season to prevent damage. In addition, periodic releases of the biological control agent can be made to provide sufficient natural enemies present for adequate control of the pest.

*Anaphes iole* (Girault) is an egg parasitoid native to north America and is specific to the eggs of *Lygus* species (Clancy and Pierce 1966, Graham et al. 1986, Sohati et al. 1992). This parasitoid has been recovered from *Lygus* eggs in a wide variety of agricultural and natural plant hosts, and studies in natural habitats indicate that it is capable of parasitizing > 90% of *Lygus* eggs in some situations. Initial cage studies of this parasitoid on *L. hesperus* in strawberry indicate that rates of parasitism up to 80% can be achieved (Norton et al. 1992). The basic biology of *A. iole* has been well studied: Jackson (1987) examined temperature effects on development and longevity; Jones and Jackson (1990) examined the effects of food on survivorship and parasitism rates; and efficient mass rearing techniques have been developed for both *A. iole* and

for *L. hesperus* (Patana and Debolt 1985). Our article reports the effect of sequential releases of *A. iole* on parasitism rates, *L. hesperus* population development, and fruit damage in commercial strawberry fields in the central coast of California.

### Materials and Methods

The impact of *A. iole* releases on *L. hesperus* population development and fruit damage was evaluated by comparing *L. hesperus* densities and fruit damage in release and nonrelease control treatments within commercial strawberry fields in Salinas and Watsonville, CA, in 1993. Three treatments were used: high release 15,000 parasitoids per plot per week (37,500/ha/wk); low release 5,000 parasitoids per plot per week (12,500/ha/wk) and control, no parasitoid releases. The 3 blocks at the Salinas site were planted with 'Selva'. At the Watsonville site, 1 block was in 'Commander' and the other in 'Swede'. Each block contained 1 replicate of each of the 3 treatments and each plot was assigned randomly to a treatment level within each of 5 blocks for a total of 15 plots. Both growers use an annual planting system and all 3 cultivars are day-neutral, producing fruit continually from early May until mid-September.

All plots were 0.4 ha in size, and separated by at least 150 m. This distance was the maximum distance that the plots within a replicate could be separated and still be contained within the same grower's field and variety, and is necessarily a trade off between maintaining treatment independence while assuring that plots are directly comparable. Previous work (unpublished data) indicates that *A. iole* is capable of moving > 80 m within 1 wk after release.

Parasitoids were distributed evenly within each plot by placing vials containing  $\approx 700$  parasitoids each beneath the plant canopy. Releases began 14 April, and continued every week until 19 August. Insufficient numbers of parasitoids were available for the first 4 wk of releases; therefore, release rates for these weeks were reduced to 5,000 per plot (high) and 0 per plot (low) on 14 and 21 April, 0 per plot (both high and low) on 28 April, and 10,000 per plot (high only) on 5 May.

None of the plots received pesticide applications for *L. hesperus* control for the duration of the experiment. Growers did use bug-vac (a large tractor mounted vacuum device) once a week for *L. hesperus* management, but vacuuming was limited to the day just before parasitoid release to minimize the impact of the machines on parasitoid survival and *Lygus* sampling. The 2 replicates at the Watsonville site were treated with abamectin (Merck, Sharp, & Dohme, Rathway, NJ) for mite control on 7 May and again on 19 May.

The *A. iole* used were produced by a commercial insectary (Biotactics, Riverside, CA). This colony originated with *A. iole* and *L. hesperus* collected from the Imperial Valley, CA, and the

Tucson, AZ, area and has been in continuous culture for  $\approx 10$  yr.

**Parasitism Rates.** Direct estimation of parasitism has proven to be extremely difficult in this system. Because *Lygus* eggs are inserted into the plant stems and occur at relatively low densities, collection of significant numbers of eggs from strawberry plants has not been successful. Instead, we estimated parasitism levels from sentinel *L. hesperus* eggs within potted strawberry plants. Use of sentinel eggs (eggs inserted into strawberry plants by *L. hesperus* females in the laboratory) has the advantage that both the age and duration of exposure can be controlled, simplifying the estimation of parasitism rates and removing potential sources of bias (i.e., different developmental rates between parasitized and unparasitized eggs or variation in host egg age at the time of sampling). Thus, parasitism rates more closely reflect the instantaneous effect of releases, rather than the sum of parasitism events for eggs of different ages and duration of exposure (Van Driesche et al. 1991). However, it should be noted that parasitism rates estimated from sentinel eggs may not accurately reflect the absolute levels of parasitism in the field because of potential differences in host-egg density, distribution (within and between plants), and duration of exposure. Because the parasitism rate of *L. hesperus* eggs by *A. iole* increases with the number of eggs in a plant (unpublished data), care was taken to insure that sentinel egg densities were within the range of field densities.

Plants with sentinel *L. hesperus* eggs were prepared by caging field-collected *L. hesperus* adults on potted strawberry plants at a density of 2 females per plant for 24 h, resulting in an average density of 1.5 eggs per plant (SD = 3.01). These plants were then placed in the release and non-release plots the following morning. Five plants were placed in the center of each plot in an X pattern, with 5 m between the nearest neighbor sentinel plant for a total of 75 plants per sample interval. Plants were located at least 5 m from the nearest release point. After 48 h, plants were returned to the laboratory and a 2nd set of plants containing *L. hesperus* eggs were placed in the field. The age of the eggs at the time of field placement was kept constant for each sample interval by staggering the placement of the plants in the oviposition cages. Following exposure in the field, the number of *L. hesperus* nymphs and *A. iole* adults successfully emerging from each plant was then recorded. Parasitism levels were determined in this manner on 3 occasions during the season: 5 May, 9 June and 14 July. For the 5 May samples, lower release rates of the parasitoids were used (10,000 per plot for the high treatment, 0 per plot for the low treatment); thus, the plants from the low release plots were omitted from the analysis. Percentage parasitism was calculated as the number of *A. iole* successfully emerging divided by the number of *L. hesperus* nymphs and *A. iole* para-

sitoids produced for each plot. ANOVA was performed on arcsine square-root transformed data using the expected sample variance ( $1/4n$ ) as a weighting factor (Sokal and Rolf 1981), and treatment, time since previous release (48 or 96 h) and sample date as independent categorical variables. Means were separated using the Scheffe' S method for multiple comparisons (Velleman 1992).

***Lygus hesperus* Densities.** Sampling for *L. hesperus* began on 7 April and was performed once a week until 2 September. Densities were determined from beat samples of 10 randomly selected plants from within each quarter of the plot and the center, for a total of five 10-plant samples per plot per week. For each sample, the number and instar of *L. hesperus* nymphs and adults was recorded. In addition to beat samples, adult densities were assessed from vacuum samples of 50 plants each week using a hand-held gasoline powered leaf vacuum (10 cm diameter opening, 5700 cm<sup>3</sup> per second air displacement). Because of the low abundance of adult *L. hesperus* found in the plots, adult densities were averaged across the 2 sampling methods to increase sample accuracy.

Differences in *L. hesperus* densities caused by *A. iole* releases were evaluated by repeated measures analysis of covariance, with parasitoid release rate as a continuous factor and site as a blocking factor. *L. hesperus* counts were natural log transformed to ensure normality, linearity, and homoscedasticity. The power of repeated measures analysis to detect within-subject effects (the effect of time on treatment or block effects) declines as the number of repeated groups increases (von Ende 1993). Therefore, *L. hesperus* counts were pooled into 2 groups to test the hypothesis that the effect of parasitoid releases was different between the 1st and 2nd generations. Counts of *L. hesperus* adults were separated into early and late season groups at the point when degree-day estimates predicted that the 1st observed nymphs would begin to become adults. Thus, early season adults are those found before the point at which the parasitoid releases could have reduced their populations and represent only those adults migrating into the plots from the surrounding environment. Because of the longevity of *L. hesperus* adults, late season individuals in this analysis include both adults produced from within the field (2nd generation adults) and older individuals from the previous generation (Strong et al. 1970, Gutierrez et al. 1977). *L. hesperus* nymphs were divided between the 2 broad peaks in nymph emergence, corresponding to the separate generations of nymphs.

**Fruit Damage.** Fruit damage levels were determined by taking all ripening fruit (any sign of red up to 75% red coloration) from a 30-plant sample from each plot each week. These fruit were then scored for *L. hesperus* damage. Even small amounts of deformity were scored as damaged; thus, damage levels reported may overestimate the amount of yield lost by growers. Percentage dam-

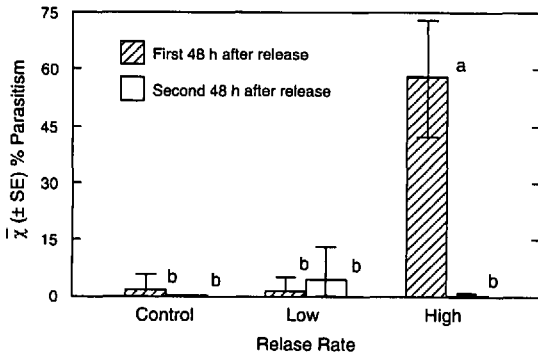


Fig. 1. Mean  $\pm$  SE parasitism of sentinel eggs first 48 h ( $\square$ ) and second 48 h ( $\square$ ) following release of *A. iole* (back-transformed) for 3 release rates. Bars followed by the same letter are not significantly different ( $P < 0.05$ ).

age was calculated as the number of damaged fruit divided by the total number of fruit in the sample for each plot. Percentage damaged fruit was analyzed by repeated measures ANOVA on un-transformed data. Examination of residuals determined that untransformed data best fit the assumptions of linearity, normality and homoscedasticity required for ANOVA. Release rate was coded as a continuous factor and block as a categorical factor. For this analysis, the total seasonal production of fruit was divided into an early and late season harvest total. Damage was estimated as the total number of damaged fruit divided by the total number of fruit produced for each plot during the interval. This method of damage estimation takes into account the fluctuations in fruit yield throughout the season and thus better reflects the total amount of yield lost than does an average of weekly damage estimates.

The effect of *L. hesperus* density on fruit damage was examined through linear regression of the percentage damaged fruit on the average number of *L. hesperus* nymphs by generation. Examination of residuals indicated that the assumptions of ANOVA were best met by untransformed variables.

**Temperatures.** Daily maximum and minimum temperatures were obtained from the University of California Integrated Pest Management Project IMPACT system from a recording station located  $\approx 1$  km from the Salinas plots and converted to degree-day accumulation using a sine wave approximation method. The expected duration of *L.*

*hesperus* generations was determined using a lower threshold for development of  $9.4^{\circ}\text{C}$  for *A. iole* and *L. hesperus* eggs (Jackson 1987) and a threshold of  $12.7^{\circ}\text{C}$  for nymphs and adults (Cave and Gutierrez 1983). Using these constants, the duration of the *L. hesperus* egg stage is 137.0 DD, 1st instar to adult is 258.4 DD, and the pre-ovipositional period is 169.5 DD.

## Results

**Parasitism Rates.** Releases of *A. iole* resulted in an increase in parasitism in sentinel eggs (Fig. 1). Release rate, time since previous release, and the interaction between these 2 variables all significantly affected parasitism, but there was no effect of sample date or block (Table 1). For the first 48 h after releases, parasitism reached high levels in the high release rate (Fig. 1), and parasitism levels were significantly different between this treatment and all others. In contrast to the high release treatment, only low levels of parasitism were observed in the low release treatments. In both treatments, only low levels of parasitism were detected in the 96-h postrelease samples. These parasitism levels were not significantly different ( $P > 0.05$ ) from control plot levels.

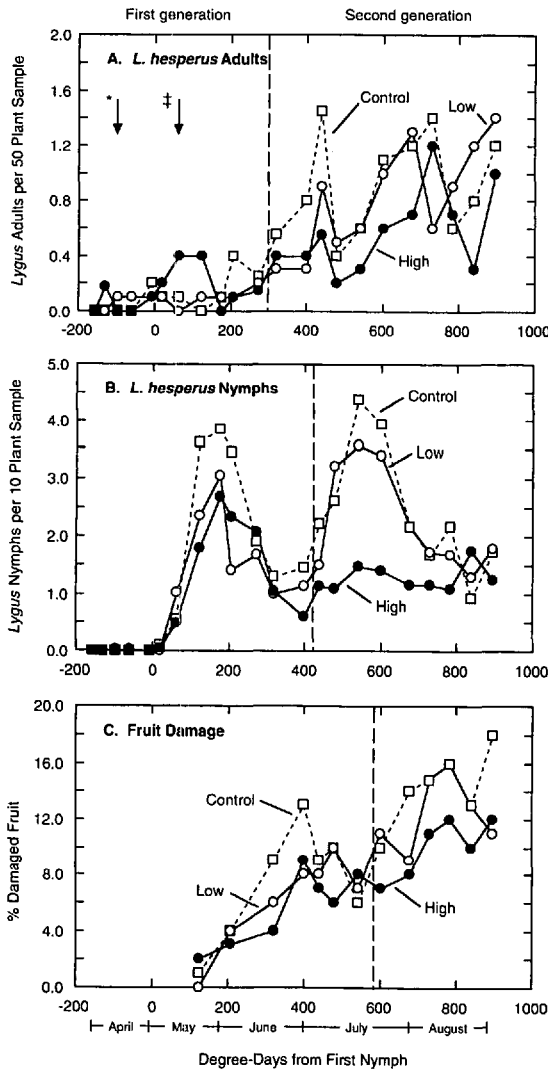
**Adult Densities.** Adult *L. hesperus* first appeared in the plots on 14 April at low levels and increased in number throughout the season (Fig. 2A). There is no significant difference in adult densities caused by parasitoid release rate over the entire season ( $P = 0.905$ ), nor is there a significant interaction between release rate and generation (early or late season) on adult densities ( $P = 0.273$ ) (Table 2). There is a slight trend to fewer adults in the 2nd generation in response to parasitoid releases and this effect appears to be greatest immediately after 2nd generation adults are predicted to appear.

**Nymph Densities.** *L. hesperus* nymphs first began to appear in the plots  $\approx 160$  DD after the appearance of adults, correlating well with degree-day estimates for egg to 1st-instar duration. There were 2 peaks in *L. hesperus* nymphs through the season, corresponding to 2 generations of *L. hesperus* for the season (Fig. 2B); however, the second peak in nymphs occurred  $\approx 2$  wk earlier than the degree-day model predicted.

Over the entire season, there was a significant reduction in the number of *L. hesperus* nymphs caused by parasitoid release (Table 3, between

Table 1. Statistical analysis of percentage parasitism

Source	SS	df	MS	F	P
Block	0.021	4	0.067	0.058	0.994
Time since previous release	1.280	1	1.280	14.315	<0.001
Release rate	2.222	2	1.111	12.427	0.000
Sample date	0.051	2	0.026	0.286	0.752
Time*Release rate	1.988	2	0.994	11.118	<0.001
Error	5.633	63			



**Fig. 2.** Phenology of *L. hesperus* adults (A), nymphs (B), and fruit damage (C) in response to releases of *A. iole*. Data values are means of 5 replicates and are plotted against degree-days > 9.4°C. □, control plots (control); ○, 5,000 *A. iole* per plot per week (low); ●, 15,000 *A. iole* per plot per week (high). The dashed vertical line separates the generations of *L. hesperus* and damage. Samples within each generation were pooled for repeated-measures ANOVA (see text for details). \*, First release of *A. iole*; †, full releases begin.

subjects effects). Nymph densities were 43% less in the high release treatment relative to controls (Fig. 3B). Repeated measures ANOVA also indicates that the effect of parasitoid releases on nymph densities changed over time. The interaction term of generation by treatment is significant ( $P = 0.077$ ; Table 3, within subjects effects). Thus, the pattern of change in nymph density between the 1st and 2nd generations is dependent upon the treatment level applied. Fig. 3B shows that on average nymph densities are higher in the 2nd generation samples for both the control and the low

**Table 2.** Statistical analysis of *Lygus* adult density

Source	SS	df	MS	F	P
Between subjects					
Block	4.964	4	1.241	1.699	0.234
Parasitoid release <sup>a</sup>	0.011	1	0.011	0.015	0.905
Error	6.573	9			
Within subjects					
Generation	14.210	1	14.210	48.390	<0.001
Generation*Block	3.424	4	0.856	2.915	0.084
Generation*Release	0.400	1	0.400	1.363	0.273
Error	2.643	9			

Repeated measures ANOVA for average density of *L. hesperus* adults, natural-log transformed. Between subject effects test the hypothesis that adult numbers are the same between source variables; within subject effects test whether the effect of a given source variable is the same between the 1st- and 2nd-generation samples. The effect of release rate × block interaction is not significant ( $P > 0.20$ ).

<sup>a</sup> One-tailed test that releases of *A. iole* reduce the numbers of adults.

release treatments, whereas nymph densities decline in the high release treatments. The interaction between block and treatment is not significant in either the between subjects or within subjects effects (Table 3). Thus, the proportional effect of parasitoid releases on *L. hesperus* nymphs was independent of the specific block examined.

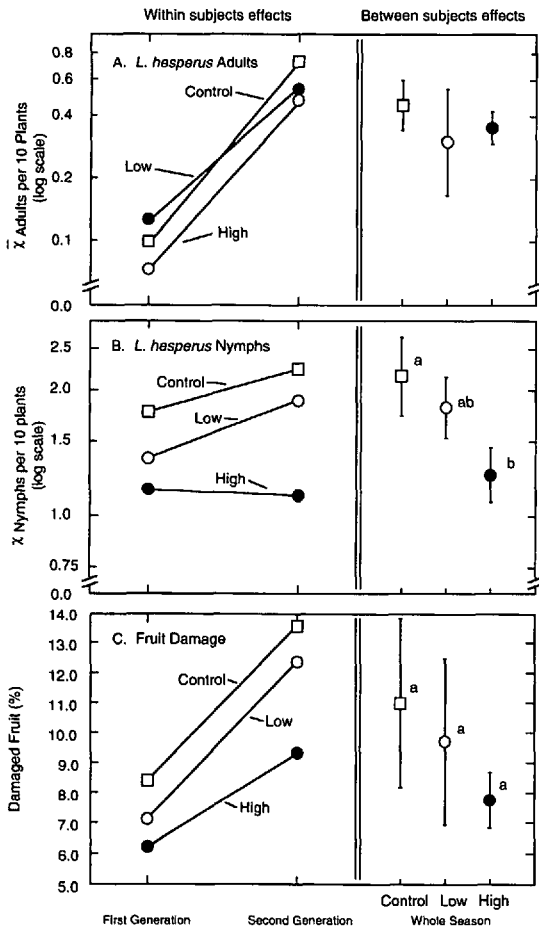
**Fruit Damage.** Levels of fruit damage in the plots follow a similar trend to those of *L. hesperus* nymphs, with 2 broad peaks in damage separated by 400 DD (Fig. 2C). Over the entire season, percentage damaged fruit was reduced in response to parasitoid releases (Table 4, between subjects effects,  $P = 0.067$ ). The effect of generation × release interactions on damage reduction is not significant (Table 4, within subjects effects,  $P = 0.520$ ). Overall, percent damaged fruit was 22% lower in the high release plots than in the controls, although mean separation techniques fail to separate damage levels caused by treatment (Fig. 3C).

**Table 3.** Statistical analysis of *Lygus* nymph density

Source	SS	df	MS	F	P
Between subjects					
Block	1.616	4	0.404	2.693	0.100
Parasitoid release <sup>a</sup>	1.628	1	1.628	10.846	0.005
Error	1.350	9			
Within subjects					
Generation	0.341	1	0.341	11.454	0.008
Generation*Block	6.256	4	1.564	52.588	<0.001
Generation*Release	0.118	1	0.118	3.978	0.077
Error	0.268	9			

Repeated measures ANOVA for average density of *L. hesperus* nymphs. Between subject effects test the hypothesis that nymph numbers are the same across source variables; within subject effects test whether the effect of a given source variable is the same between the 1st- and 2nd-generation samples. The effect of release rate × block interaction is not significant ( $P > 0.20$ ).

<sup>a</sup> One-tailed test that releases of *A. iole* reduce the numbers of nymphs.



**Fig. 3.** Graphical representation of repeated-measures analyses. *L. hesperus* adults (A), nymphs (B), and fruit damage (C). Points are back-transformed from natural-log data. □, control plots (control); ○, 5,000 *A. iole* per plot per week (low); ●, 15,000 *A. iole* per plot per week (high). Each point is the average for the given sample interval. The left hand portion of each graph illustrates the within subjects effects (changes in number between generations by treatment applied). The right hand portion represents the between subjects effects (the effect of treatment on population response for the entire season). Vertical bars represent standard errors ( $n = 5$ ). Points followed by a common letter are not significantly different at the 5 % level (Scheffé mean separation).

The amount of damaged fruit increases with the average number of *L. hesperus* nymphs found over all plots, and this relationship is linear over the range of *L. hesperus* nymphs observed (Fig. 4). The relationship between nymph densities and fruit damage found here is intermediate between 2 other estimates of this relationship. The data from Pickel et al. (1991) (who used similar sampling methods) indicates a steeper relationship between *L. hesperus* densities and damage. However, in a manipulative study of the relationship between nymphs and damage Zalom et al. (1990) found

**Table 4.** Statistical analysis of percentage damaged fruit

Source	SS	df	MS	F	P
Between subjects					
Block	0.047	4	0.012	6.176	0.011
Parasitoid release <sup>a</sup>	0.005	1	0.005	2.732	0.067
Error	0.017	9			
Within subjects					
Generation	0.010	1	0.010	7.624	0.022
Generation*Block	0.026	4	0.006	4.724	0.025
Generation*Release	0.001	1	0.001	0.449	0.520
Error	0.012	9			

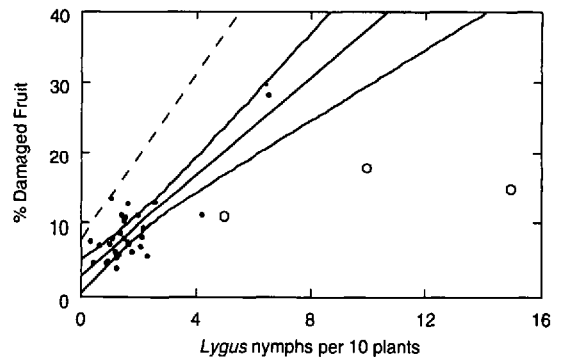
Repeated measures ANOVA for percentage fruit damage. Between subject effects test the hypothesis that the amount of fruit damage is the same across source variables; within subject effects test whether the effect of a given source variable is the same between the 1st- and 2nd-generation samples. The effect of release rate  $\times$  block interaction was not significant ( $P > 0.20$ ).

<sup>a</sup> One-tailed test that releases of *A. iole* reduce the amount of damaged fruit.

much less damage occurred for a given density of nymphs.

**Discussion**

Parasitism levels increased following releases of *A. iole*, though this effect was temporary and declined sharply after 48 h (Fig. 1). Two factors may contribute to this decline. *A. iole* is able to disperse rapidly following a single mass release (unpublished data), and the reduction in parasitism found 48 h after a release may reflect dispersal of the parasitoids through the field and a reduction in the number of adult parasitoids within the test plots. Another contributing factor is that *A. iole* adults are short lived, with an average longevity of 67.3 DD (Jackson 1987). This equates to slightly longer than 1 wk under the conditions found in this experiment. Thus, the first 48 h following release



**Fig. 4.** Linear regression of percentage damaged fruit against *L. hesperus* nymph density. Data were pooled by generation for analysis (see Fig. 2). ●, data values from this experiment; solid lines are the resulting regression equation and 95% CI ( $y = 2.858 (\pm 0.902) + 3.492 (\pm 0.383) x$ ;  $R^2 = 0.748$ ;  $P < 0.001$ ,  $n = 15$ ). ○, values from Zalom et al. (1990); the upper (dashed) regression line was generated from data in Pickel et al. (1991).

constitutes a relatively large portion of the total adult life span of the parasitoid and mortality may act to limit the duration of a release effect.

These 2 hypotheses have opposite implications for the success of a mass release strategy. The ability of a parasitoid to disperse following release may be advantageous because fewer releases per unit area of field would need to be made to ensure an even distribution of the parasitoid (King et al. 1985). If dispersal is a major component of the reduction in parasitism through time, we would also expect that greater levels of parasitism and nymph reduction would be obtained as the size of test plots is increased (Schneider 1989). However, if low parasitoid longevity is responsible for the decline in parasitism, control of the pest would only be enhanced by increasing the frequency or size of releases.

Low levels of parasitism were found in the control plots (Fig. 1), and it is not clear whether this resulted from indigenous parasitoids or from movement of released parasitoids into the control plots. In similar release experiments (unpublished data), low levels of parasitism (< 5%) were found in control plots as well. Because none of the plots were treated with insecticides for *L. hesperus* management, pesticide use does not appear to be causing these low levels of parasitism from *A. iole*. However, it is possible that other chemicals used in strawberries (such as acaricides or fungicides) or the frequent use of the bug-vac limit the colonization of strawberry fields by *A. iole*.

Other hypotheses not addressed in this experiment may explain the low levels of background parasitism: the low levels of parasitism found in strawberries may reflect low levels of *A. iole* in central California in general, or that the high level of mobility exhibited by *L. hesperus* adults allows for escape through space from populations of the parasitoid. This latter hypothesis may be particularly appropriate in the case of large scale production agriculture which is largely isolated from areas of natural *Lygus* spp. host plants. Augmentation of *A. iole* may be the most efficient way of increasing mortality levels from this natural enemy.

This experiment did not detect any significant reduction in the 2nd-generation *L. hesperus* adults as a result of parasitoid releases (Fig. 3A; Table 2). Because of the highly mobile nature of *Lygus* spp. adults (Fliesher et al. 1988) and the tendency of females to disperse following egg maturation, parasitoid effects on adult densities may not be detectable at the spatial scale of this experiment. Larger sized plots would be required to determine if *A. iole* reduces the density of 2nd generation adults and if such an effect would translate into fewer subsequent *L. hesperus* nymphs for a grower using biological control.

Because of the longevity of the adult stage of *L. hesperus*, samples during the latter half of the season include both adults from the 1st generation and the 2nd generation, making an effect on adult

densities even more difficult to detect. The low densities of *L. hesperus* in the plots coupled with large amounts of variability caused by sampling imprecision may also obscure any effect.

Increased parasitism following *A. iole* releases led to a reduction in *L. hesperus* nymphs and this effect increased with time in the high release plots (Fig. 3B). There are several possible explanations for the greater reduction of *L. hesperus* in the latter half of the season. Parasitoid densities may have been higher in the 2nd half of the season as the progeny from early releases of *A. iole* began to emerge and thus higher parasitoid densities resulted in greater control of *L. hesperus*. Alternatively, the lower release rates used in the 1st few weeks of the experiment could have resulted in a reduced parasitoid effect during the 1st half of the season.

It is also possible that the parasitoid releases resulted in a decrease in the number of 2nd-generation *L. hesperus* females in the high release treatment. Fewer 2nd generation adults would result in fewer *L. hesperus* nymphs. This hypothesis does not seem likely, because no significant effect of parasitoid release on second generation *L. hesperus* adults was detected, and the average number of adults was similar between treatments. Finally, the better control of *L. hesperus* in the latter half of the season may reflect greater parasitoid efficiency. In general, late season temperatures were higher than in the beginning of the season and there were fewer incidents of precipitation or heavy dew. Parasitoid effectiveness may have been enhanced under the climatic conditions found during the 2nd generation of *L. hesperus*. However, experiments designed to specifically test these hypotheses need to be performed to fully evaluate them.

Grower use of the bug-vac may have reduced both *L. hesperus* and *A. iole* densities in these experiments (Pickel et al. 1994). Because vacuum use was limited to the day before parasitoid release and parasitism declines rapidly after 48 h, vacuum impact was likely greater on *L. hesperus* populations than on *A. iole*. At the time these experiments were performed, it was not possible to find strawberry growers willing to permit experimentation on relatively large blocks of strawberries in the absence of any *L. hesperus* control measures. Although use of Bug-vac by growers may have changed the absolute magnitude of the response variables, vacuum use was applied evenly across all treatments and the general conclusion of less nymphs and less damage in response to parasitoid releases remains valid.

The observed reduction in damage levels following parasitoid releases was not as robust as the reduction in nymphs (Fig. 3C). Although the data indicate that there was a reduction in the amount of damage as release rate increased, mean separation techniques failed to find differences in response to treatment level. This may be the result

of the relatively low power of statistical tests with only 5 replicates. This factor coupled with variation in the relationship between parasitoid releases and nymph densities and variation in the relationship between nymph densities and fruit damage reduces the sensitivity of the statistical test used. Because *A. iole* releases affect damage levels through a reduction in *L. hesperus* nymphs (instead of acting directly on fruit damage), greater variability and thus lower probability of rejecting the null hypothesis is expected. However, there is a trend to greater parasitism levels and decreases in nymph density and fruit damage in response to release rate.

Across all treatments, average *L. hesperus* densities correlated well with the amount of damage observed (Fig. 4). The relationship between *L. hesperus* nymphs and fruit damage found here is intermediate between 2 other experiments performed with day-neutral cultivars in California (Zalom et al. 1990, Pickel et al. 1991), although differences in sampling techniques and experimental protocols make direct comparison difficult. The significant positive intercept value for this relationship (the amount of damaged expected if no *L. hesperus* nymphs are present) may have biological significance as well. Other sources of fruit deformity, such as nutrient deficiencies (Ulrich et al. 1992), poor pollination (Vincent et al. 1990) or other insects may contribute to deformity that we were not able to distinguish from *L. hesperus* feeding.

Left untreated, *L. hesperus* nymphs are capable of causing substantial amounts of damage. The current treatment threshold recommended by the University of California IPM Project (1994) is 0.5 nymphs per 10 plants using the beat sampling method. Using the regression equation found here, an average density of one-half nymph per 10 plants would result in an additional 1.75% damage over background levels. Maintaining population levels below this level would require the use of multiple insecticide applications (Zalom et al. 1990; personal observation), and it is questionable whether this threshold is practical or cost effective given both the cost of pesticide applications and the potential for yield reductions as a result of disruption of mite control programs. Using published USDA-ERS statistics from 1993, a 1% reduction in yield over the portion of the season when *L. hesperus* is active would result in a reduction in gross revenues of \$178 per acre (\$445/ha) (USDA-ERS 1995). Thus, there are very real economic incentives for growers to minimize yield reductions caused by any pest.

These results demonstrated that mass releases of *A. iole* reduced the development of populations of *L. hesperus* nymphs and the subsequent fruit damage, and thus this parasitoid may prove to be an effective management tool for this pest. At the high release rate parasitism levels increased and *L. hesperus* nymphs and fruit damage were reduced.

These results suggest that releases of *A. iole* represent a biologically viable tool for *L. hesperus* management. As with all pest management techniques, determination of efficacy is a necessary step in the development of strategies that are useful to the end user. The next step in this process is the evaluation of both costs and benefits of parasitoid augmentation and other existing strategies for *L. hesperus* management.

#### Acknowledgments

We thank Matt Clark, Kelly Wood, and Ruth Hufbauer (Department of Environmental Science, Policy and Management, University of California, Berkeley), for assistance in executing this research, and Glenn Scriven (Bio-tactics) for parasitoid rearing, Nick J. Mills (University of California, Berkeley, Department of Environmental Science, Policy and Management) and Wayne P. Sousa (University of California, Berkeley, Department of Integrative Biology) provided insightful comments on earlier versions of the manuscript. This research was funded by the University of California Integrated Pest Management Program, the California Strawberry Commission, and a USDA Small Business Innovation Research grant to Bio-tactics.

#### References Cited

- Allen, W. W., and S. E. Gaede. 1963. The relationship of *Lygus* bugs and thrips to fruit deformity in strawberries. *J. Econ. Entomol.* 56: 823-826.
- Butts, R. A., and R. J. Lamb. 1991. Pest status of lygus bugs (Hemiptera: Miridae) in oilseed Brassica crops. *J. Econ. Entomol.* 84: 1591-1596.
- Cave, R. D., and A. P. Gutierrez. 1983. *Lygus hesperus* field life table studies in cotton and alfalfa (Heteroptera: Miridae). *Can. Entomol.* 115: 649-654.
- Clancy, D., and H. Pierce. 1966. Natural enemies of some *Lygus* bugs. *J. Econ. Entomol.* 59: 853-858.
- Day, W. H., R. C. Hedlund, L. B. Saunders, and D. Coutinot. 1990. Establishment of *Peristenus digoneutis* (Hymenoptera: Braconidae), a parasite of the tarnished plant bug (Hemiptera: Miridae), in the USA. *Environ. Entomol.* 19: 1528-1533.
- Fleischer, S. J., and M. J. Gaylor. 1987. Seasonal abundance of *Lygus lineolaris* (Heteroptera: Miridae) and selected predators in early season uncultivated hosts: implications for managing movement into cotton. *Environ. Entomol.* 16: 379-389.
- Fleischer, S. J., M. J. Gaylor, and N. V. Hue. 1988. Dispersal of *Lygus lineolaris* (Heteroptera: Miridae) adults through cotton following nursery host destruction. *Environ. Entomol.* 17: 533-541.
- Graham, H. B., C. G. Jackson, and J. W. Debolt. 1986. *Lygus* spp. (Hemiptera: Miridae) and their parasites in agricultural areas of southern Arizona. *Environ. Entomol.* 15: 132-142.
- Gutierrez, A. P., T. F. Leigh, Y. Wang, and R. D. Cave. 1977. An analysis of cotton production in California: *Lygus hesperus* (Heteroptera: Miridae) injury—an evaluation. *Can. Entomol.* 109: 1375-1386.
- Hedlund R. C., and H. B. Graham. 1987. Economic importance and biological control of *Lygus* and *Adelphocoris* in North America. U.S. Dep. Agric. Agric. Res. Serv. 64.



- Jackson, C. G. 1987.** Biology of *Anaphes oviventatus* (Hymenoptera: Mymaridae) and its host, *Lygus hesperus* (Hemiptera: Miridae), at low and high temperatures. *Ann. Entomol. Soc. Am.* 80: 367-372.
- Jones, W. A., and C. G. Jackson. 1990.** Mass production of *Anaphes iole* for augmentation against *Lygus hesperus*: effects of food on fecundity and longevity. *Southwest. Entomol.* 15: 463-468.
- King, E. G., K. R. Hopper, and J. E. Powell. 1985.** Analysis of systems for biological control of crop pests in the U.S. by augmentation of predators and parasites, pp. 201-227. *In* M. A. Hoy and D. C. Herzog [eds.], *Biological control in agricultural IPM systems*. Academic, Orlando, FL.
- Leigh, T. A., and P. F. Wynholds. 1988.** Cotton square damage by the plant bug, *Lygus hesperus* (Hemiptera: Heteroptera: Miridae), and abscission rates. *J. Econ. Entomol.* 81: 1328-1337.
- Norton, A. P., S. C. Welter, J. L. Flexner, C. G. Jackson, J. W. Debolt, and C. Pickel. 1992.** Parasitism of *Lygus hesperus* (Miridae) by *Anaphes iole* (Mymaridae) and *Leiophron uniformis* (Braconidae) in California strawberry. *Biol. Control* 2: 131-137.
- Parrella, M. P., K. M. Heinz, and L. Nunney. 1992.** Biological control through augmentative releases of natural enemies: a strategy whose time has come. *Am. Entomol.* 38: 172-179.
- Patana, R., and J. W. Debolt. 1985.** Rearing *Lygus hesperus* in the laboratory. *U.S. Dep. Agric. Agric. Res. Serv.* 45.
- Pickel, C., N. C. Welch, J. Becker, F. Zalom, and D. B. Walsh. 1991.** Innovative mite and *Lygus* control research. Annual Report of Strawberry Research. California Strawberry Advisory Board, Watsonville, CA.
- Pickel, C., F. G. Zalom, D. B. Walsh, and N. C. Welch. 1994.** Efficacy of vacuum machines for *Lygus hesperus* (Hemiptera: Miridae) control in coastal California strawberries. *J. Econ. Entomol.* 87: 1636-1640.
- Schaefers, G. A. 1966.** The reduction of insect-caused apical seediness in strawberries. *J. Econ. Entomol.* 59: 698-706.
- Schneider, J. C. 1989.** Role of movement in evaluation of area-wide insect pest management tactics. *Environ. Entomol.* 18: 868-874.
- Schwartz, M. D., and R. G. Foottit. 1992.** *Lygus* bugs on the prairies: biology, systematics and distribution. *Agric. Can. Tech. Bull.* 1992-4E.
- Snodgrass, G. L., W. P. Scott, and J. W. Smith. 1984.** An annotated list of the host plants of *Lygus lineolaris* (Hemiptera: Miridae) in the Arkansas, Louisiana, and Mississippi delta. *J. Ga. Entomol. Soc.* 19: 93-101.
- Sohati, P. H., G. Boivin, and R. K. Stewart. 1992.** Parasitism of *Lygus lineolaris* eggs on *Coronilla varia*, *Solanum tuberosum*, and three host weeds in southeastern Quebec. *Entomophaga* 37: 515-523.
- Sokal, R. R., and F. J. Rolf. 1981.** *Biometry*. Freeman, New York.
- Sorenson, C. J. 1936.** *Lygus* bugs in relation to shriveled alfalfa seed. *J. Econ. Entomol.* 29: 454-457.
- Stewart, S. D., and M. J. Gaylor. 1994.** Effects of age, sex, and reproductive status on flight by the tarnished plant bug (Heteroptera: Miridae). *Environ. Entomol.* 23: 80-84.
- Stitt, L. L. 1949.** Host-plant sources of *Lygus* spp. infesting the alfalfa seed crop in southern Arizona and southeastern California. *J. Econ. Entomol.* 42: 93-99.
- Strong, F. E., J. A. Sheldahl, P. R. Highes, and E. M. K. Hussein. 1970.** Reproductive biology of *Lygus hesperus* Knight. *Hilgardia* 40: 105-147.
- Ulrich, A., M. A. E. Mostafa, and W. W. Allen. 1992.** Strawberry deficiency symptoms: a visual and plant analysis guide to fertilization. University of California, Division of Agricultural Sciences, Oakland.
- University of California Integrated Pest Management Project. 1994.** Integrated pest management for strawberries. Division of Agriculture and Natural Resources, University of California, Oakland, CA.
- [USDA-ERS.] U.S. Department of Agriculture, Economic Research Service. 1995.** The U.S. Strawberry Industry. USDA-ERS, Washington, DC.
- Van Driesche, R. C., T. S. J. Bellows, J. S. Elkinton, J. R. Gould, and D. N. Ferro. 1991.** The meaning of percentage parasitism revisited: solutions to the problem of accurately estimating total losses from parasitism. *Environ. Entomol.* 20: 1-7.
- Velleman, P. F. 1992.** *Data desk handbook*. Data Description, Ithaca, NY.
- Vincent, C., D. D. de Oliveira, and A. Belanger. 1990.** The management of insect pollinators and pests in Quebec strawberry plantations. *In* N. J. Bostanian, L. T. Wilson, and T. J. Dennehy [eds.], *Monitoring and integrated management of arthropod pests of small fruit crops*. Intercept, Andover, Hampshire, UK.
- von Ende, C. N. 1993.** Repeated-measures analysis: growth and other time dependent measures. *In* S. M. Scheiner and J. Gurevitch [eds.], *Design and analysis of ecological experiments*. Chapman & Hall, New York.
- Young, O. P. 1986.** Host plants of the tarnished plant bug, *Lygus lineolaris* (Heteroptera: Miridae). *Ann. Entomol. Soc. Am.* 79: 747-762.
- Zalom, F. G., C. Pickel, and N. C. Welch. 1990.** Recent trends in strawberry arthropod management for coastal areas of the western United States. *In* N. J. Bostanian, L. T. Wilson, and T. J. Dennehy [eds.], *Monitoring and integrated management of arthropod pests of small fruit crops*. Intercept, Andover, Hampshire, UK.

Received for publication 22 September 1995; accepted 11 July 1996.