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The contribution of conservation biological control to integrated control of *Bemisia tabaci* in cotton ☆

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ABSTRACT

Integrated control systems are based on the complimentary contribution of chemical and biological control fostered by conservation of natural enemies. Yet, in the 50 years since the integrated control concept [ICC] [Stern, V.M., Smith, R.F., van den Bosch, R., Hagen, K.S., 1959. The integrated control concept. Hilgardia 29, 81–101] was introduced there are few operational programs and even fewer attempts to analyze the mechanisms that allow chemical and biological control to act in concert. The dearth of demonstrable evidence for the ICC has eroded the credibility of biological control and its usage in operational IPM plans. We used *in situ* life tables within an experimental design to measure and compare the contribution and interaction of biological control and insecticides as tactical components within three pest management systems for *Bemisia tabaci* (Gennadius) in cotton. Insecticides were the key factor immediately following applications of broad-spectrum materials or one of two selective insect growth regulators (IGRs), and this mortality replaced that provided by natural enemies. Two to six weeks later, however, mortality from natural enemies, primarily predation, in the IGR regimes rebounded to the high levels observed in untreated controls and became the key factor. Mortality from natural enemies remained depressed in the broad-spectrum insecticide regime. Single IGR applications were sufficient to suppress *B. tabaci* populations throughout the season, while up to five broad-spectrum applications were needed to achieve comparable control. The chemical residual of IGRs was limited to several weeks, demonstrating a key role for mortality from conserved natural enemies that extended the control interval. This "bioresidual" allows for long-term, commercially-acceptable pest suppression following the use of selective insecticides. We provide a rare experimental illustration of integrated control, where chemical and biological controls "augment one another". Our approach and methodology could be applied to demonstrate and validate integrated control in many other systems, addressing a critical need for implementation of biological control in practicing IPM systems.

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1. Introduction

The goal of conservation biological control is to modify the environment such that the abundance and associated activity of biological control agents are enhanced, leading to improved pest management. This goal can be achieved by manipulating the environment to favor natural enemies of the target pest either by enhancement of the habitat through the addition of resources and/or by removing or mitigating adverse factors (van den Bosch and Telford, 1964; DeBach, 1974; Ehler, 1998; Gurr and Wratten, 1999; Landis et al., 2000). Many factors may cause agricultural environments to be unsuitable for natural enemies, and as a result, hinder their contribution to pest suppression. This includes adverse climate and microclimate, scarcity of water and supplemental foods like nectar and pollen and/or alternate prey, competition, intraguild predation, physical and chemical attributes of the crop plant, lack of sufficient shelter, adverse cultural practices, and use of broad-spectrum insecticides (DeBach and Hagen, 1964; van den Bosch and Telford, 1964; Rabb et al., 1976; Croft, 1990). This latter factor is perhaps most significant in disrupting biological control of arthropod pests in most cropping systems and led to the foundation of the integrated control concept (Stern et al., 1959). Biological control, when insecticides also play an important role in pest suppression, will depend on the use of more selective materials and/or more biorational approaches with broader-spectrum insecticides to minimize their effects on natural enemies (Stern et al., 1959; Newsom et al., 1976; Hull and Beers, 1985; Croft, 1990; Johnson and Tabashnik, 1999). A biorational approach should have little or no adverse effects in the ecosystem while augmenting control of the target pest (Horowitz et al., 2009).

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Many studies have examined the putative selectivity of various insecticides and application methods on natural enemy populations in both the laboratory and the field (see Croft, 1990; Ruberson et al., 1998 and Johnson and Tabashnik, 1999 for reviews), but there has been little effort to measure the value of selectivity in terms of more efficient population regulation by conserved natural enemies (Waage, 1989). Fifty years ago, Stern et al. (1959) asserted that, "Few studies have included basic investigations on the effects the chemicals might have on other components of the ecosystems to which the pests belong." This statement holds true today where few do integrative studies of chemical control where multiple factors, especially those responsible for pest mortality, are examined contemporaneously within the full ecological context of the control system. For example, Jaynes and Marucci (1947) showed that parasitism and predation on sentinel and natural codling moth prey were generally higher in unsprayed apple orchards compared with commercially sprayed orchards. More recently, Furlong et al. (2004) used life table analyses in exclusion cage studies to show that rates of diamondback moth survival on cabbage was generally lower and natural enemy-induced mortality higher when growers used more IPM intensive methods rather than more frequent calendar sprays of broad-spectrum insecticides in Australia. In contrast, Sarvary et al. (2007) found that rates of predation and parasitism of sentinel obliquebanded leafroller larvae were similar in apple orchards using reduced-risk insecticides compared with those using conventional materials even though populations of natural enemies were generally higher in reduced-risk orchards. To our knowledge, no studies have attempted to compare and quantify multiple mortality rates and their interactions for insect pests when applying different management strategies. More specifically, and within the context of integrated control, there has been no attempt to quantitatively measure the contributions of biological and chemical control.

Bemisia tabaci (Gennadius) [Hemiptera: Aleyrodidae] biotype B (= *B. argentifolii* Perring & Bellows) is a major pest of numerous crops worldwide. In cotton, feeding damage by *B. tabaci* reduces lint yields, and honeydew deposition can lead to significant reductions in lint quality from stickiness and discoloration from associated sooty molds (Hector and Hodkinson, 1989; Naranjo et al., 1998). Management strategies for *B. tabaci* on cotton in the western USA are based in part on pest monitoring and use of economic thresholds to determine the need for insecticides (Ellsworth et al., 1995, 1996; Naranjo et al., 1998). The current system is based around the initial prescriptive use of selective insecticides such as the two insect growth regulators (IGRs), buprofezin, a chitin synthesis inhibitor, and pyriproxyfen, a juvenile hormone analog, that has allowed successful management of *B. tabaci* for over 12 years (Ellsworth and Jones, 2001; Ellsworth and Martinez-Carrillo, 2001; Ellsworth et al., 2006). Extensive field testing has demonstrated that these IGRs are not only highly effective against *B. tabaci* but also very selective, fostering conservation of natural enemies (Naranjo et al., 2003, 2004) and potentially conservation biological control.

A large assemblage of predators, parasitoids and fungi (Lopez-Avila, 1986; Breene et al., 1994; Lacey et al., 1996; Gerling et al., 2001) are known to attack *B. tabaci* in a number of agricultural systems. Some evidence suggests these natural enemies play an important role in the control of *B. tabaci*. Several studies have documented resurgence of *B. tabaci* in cotton with use of broad-spectrum insecticides (e.g., Abdelrahman and Munir, 1989; Devine et al., 1998; Asiimwe, Ellsworth and Naranjo, unpublished data), and a few have shown that generalist predators and aphelinid parasitoids act as key factors in the population dynamics of this pest in several crops in the absence of insecticides (Naranjo and Ellsworth, 2005; Asiimwe et al., 2006; Karut and Naranjo, 2009; Naranjo, Ellsworth and Cañas, unpublished data). Despite the high rates of mortality imposed by predators, parasitoids and other natural forces, insecticides are typically needed to maintain populations of *B. tabaci* below economically damaging levels (Naranjo, 2001; Ellsworth and Martinez-Carrillo, 2001). Our hypothesis is that the use of selective insecticides that conserve natural enemies should allow these agents to make an important contribution to pest control and perhaps reduce overall insecticide inputs for all pests in the system.

Life tables and their associated analyses are a robust methodology for assessing the impact of natural enemies on pest populations, especially within an experimental context (Bellows et al., 1992; Bellows and Van Driesche, 1999). Many factors are known to cause mortality in populations of *B. tabaci* (Naranjo and Ellsworth, 2005) and life table studies help structure, quantify, and interpret mortality factors and interactions among mortality sources in pest management systems. The objective of this study was to measure sources and rates of *B. tabaci* mortality due to natural enemies, insecticides and other factors under different pest management strategies using *in situ* life tables. Over a three year period, life tables were constructed for immature stages of *B. tabaci* in large experimental plots that were used to contrast and demonstrate alternative management strategies for *B. tabaci* in Arizona cotton. These strategies were based on pest monitoring, economic thresholds, and the use of either the selective IGRs buprofezin and pyriproxyfen, or conventional broad-spectrum insecticides. Our goal was to quantify the contribution of conserved natural enemies towards commercially-acceptable pest suppression within the context of other interacting mortality forces impacting the population dynamics of *B. tabaci*. The intended outcome was an informed clientele that could immediately implement "integrated control", and restoration of interest and confidence in the conserved biological control elements of the Arizona cotton pest management system.

2. Materials and methods

2.1. Study site and experimental design

Studies were conducted at the University of Arizona, Maricopa Agricultural Center, Maricopa, AZ (latitude: 33.06902° north, longitude: 111.97230° west, elevation: 360.0 m). Cotton, *Gossypium hirsutum* L. (cv. Deltapine NuCOTN 33B), was planted in early to mid-April each year, and grown according to standard agronomic practices for the area, which included application of pre-plant herbicides, level furrow irrigation at a total rate of ≈91 cm of water per hectare applied every 10–14 days, periodic cultivation for weed control and bed reshaping, and a total of 45–68 kg of N applied as three side-dresses at approximately monthly intervals beginning in mid June.

Similar experimental designs were used in all years and consisted of a randomized complete block, split-plot replicated four times. Whole plots consisted of one of three *B. tabaci* control regimes and an untreated control. In 1997, whole plots were 24–27 rows wide (1 m row-spacing) by 45.7 m long (0.11–0.12 ha). In 1998 and 1999 whole plots measured 36 rows by 36.6 m long (0.13 ha). Each whole plot was split for two *Lygus hesperus* Knight [Hemiptera: Miridae] control regimes, untreated or treated with insecticides. Split-plots were 12 rows by 45.7 m (0.055 ha) in 1997 and 18 rows by 36.6 m (0.065 ha) in 1998 and 1999. The whole plot whitefly management regimes are denoted by the initial materials used in each regime, and all applications were made on the basis of regular insect sampling and economic thresholds (Table 1). In the buprofezin-first regime, the IGR buprofezin was applied at a threshold of one large nymphal whitefly (third or fourth instar) per leaf disk plus 3–5 adult whiteflies per leaf (see Pest Sampling below) (Ellsworth et al., 1996). This was followed

Table 1
Insecticide application history, Maricopa Agricultural Center, Maricopa, AZ, 1997–1999.

Date	Main plot treatment			
	Buprofezin 1st	Pyriproxyfen 1st	Conventional	Control
1997				
25 July	Oxamyl[a] (1121 g/ha)	Oxamyl[a] (1121 g/ha)	Oxamyl[a] (1121 g/ha)	Oxamyl[a] (1121 g/ha)
29 July	Buprofezin (392 g/ha)	Pyriproxyfen (60 g/ha)	Endosulfan (841 g/ha) + amitraz (280 g/ha)	
5 August			Oxamyl (561 g/ha) + profenophos (841 g/ha)	
20 August			Fenpropathrin (224 g/ha) + acephate (561 g/ha)	
4 September			Endosulfan (841 g/ha) + amitraz (280 g/ha)	
12 September			Fenpropathrin (224 g/ha) + oxamyl (561 g/ha)	
1998				
17 July	Oxamyl[a] (1121 g/ha)	Oxamyl[a] (1121 g/ha)	Oxamyl[a] (1121 g/ha)	Oxamyl[a] (1121 g/ha)
31 July	Acephate[a] (1121 g/ha)	Acephate[a] (1121 g/ha)	Acephate[a] (1121 g/ha)	Acephate[a] (1121 g/ha)
6 August	Buprofezin (392 g/ha)	Pyriproxyfen (60 g/ha)	Endosulfan (841 g/ha) + amitraz (280 g/ha)	
17 August	Oxamyl[a] (1121 g/ha)	Oxamyl[a] (1121 g/ha)	Oxamyl[a] (1121 g/ha)	Oxamyl[a] (1121 g/ha)
1999				
20 July	Oxamyl[a] (1121 g/ha)	Oxamyl[a] (1121 g/ha)	Oxamyl[a] (1121 g/ha)	Oxamyl[a] (1121 g/ha)
29 July	Acephate[a] (1121 g/ha)	Acephate[a] (1121 g/ha)	Acephate[a] (1121 g/ha)	Acephate[a] (1121 g/ha)
8 August	Buprofezin (392 g/ha)	Pyriproxyfen (60 g/ha)	Endosulfan (841 g/ha) + amitraz (280 g/ha)	
13 August	Oxamyl[a] (1121 g/ha)	Oxamyl[a] (1121 g/ha)	Oxamyl[a] (1121 g/ha)	Oxamyl[a] (1121 g/ha)
27 August			Oxamyl (561 g/ha) + profenophos (841 g/ha)	
10 September			Fenpropathrin (224 g/ha) + acephate (561 g/ha)	

All rates given in grams of active ingredient per hectare.
[a] Insecticides used for control of *L. hesperus*; applied to only one-half of the main treatment plots in a split-plot design.

by the use of the IGR pyriproxyfen based on the same threshold, but no sooner than 2 weeks following the application of buprofezin. The pyriproxyfen-first regime consisted of the use of pyriproxyfen according to the same thresholds above with a follow-up application of buprofezin as needed, but no sooner than 3 weeks following pyriproxyfen. The waiting period between IGR uses was mandated by the US-EPA Section 18 labels in force at the time (Ellsworth and Martinez-Carrillo, 2001). These labels also permitted only a single use of each IGR per season. While the buprofezin label in cotton now permits up to two uses, the original IGR "rules" are still taught to growers as guidelines today (Ellsworth et al., 2006). If additional suppression was needed in either of these IGR regimes, a rotation of conventional insecticides was used based on a threshold of five adult whiteflies per leaf (Ellsworth et al., 1995). The conventional control regime consisted of mixtures of conventional materials rotated each time according to local resistance management guidelines and based on a threshold of five adult whiteflies per leaf (Ellsworth et al., 1995, 1996). A final regime was left untreated for *B. tabaci* to serve as the control. In the treated split-plots, insecticide applications for *L. hesperus* were made on the basis of a threshold of 15 insects (adults + nymphs) per 100 sweeps. Sprays rotated between oxamyl and acephate as needed. These insecticides alone have no practical efficacy against *B. tabaci*. The remaining split was left untreated for *L. hesperus*. All applications were made by tractor-mounted ground sprayers. Seasonal usage of insecticides is summarized in Table 1.

2.2. Life table methods

2.2.1. Cohort establishment

Bemisia tabaci is a multivoltine insect without a quiescent stage, leading to broadly overlapping generations throughout the year. To avoid the inherent problems of attempting to estimate stage recruitment and mortality from frequent population censuses, we used an *in situ* observational method that took advantage of the sessile nature of the immature stages of this insect. Cohorts of eggs (<1 day old) were established from natural populations on the underside of cotton leaves. Newly-laid eggs were identified by their creamy white color and their location on leaves near the terminal of the cotton plant. An 8X Peak loupe (Light Impressions, Brea, CA, USA) commonly used for viewing slides or 35 mm film, was used to locate eggs and a non-toxic, ultra-fine-point black permanent marker (Sanford, Bellwood, IL, USA) was used to draw a small circle around individual eggs or small clusters of no more than 2–3 eggs. Preliminary studies in the laboratory indicated that the mark did not differentially affect the behavior of foraging generalist predators or aphelinid parasitoids. A small slot was cut in the side of the loupe so that the marking pen could be inserted and manipulated within the field of view. A small numbered white tag was placed around the petiole of the leaf containing the marked eggs and a short length of non-attractive red or white plastic flagging tape was tied around the mainstem of the plant to facilitate relocation. No more than five eggs were marked on a single leaf and only a single leaf was used per plant. Plants were evenly spaced along the central 2–3 rows of each plot. The three main veins of the leaf were used to establish quadrants and further refine the location of individual eggs for subsequent observations. A minimum of 50 eggs were marked in each plot or split-plot for each date. As many as 30–40 leaves (and plants) were used per plot, depending on insect density. An identical procedure was used to locate and mark the position of newly settled 1st instar nymphs with the exception that marked circles never contained more than one nymph. Settled 1st instars could be readily distinguished from crawlers by having a slightly more translucent color and being flush with the leaf surface. To verify that settled nymphs and not crawlers were marked, we re-examined each marked individual after about 1–5 h. Again, a minimum of 50 nymphs were marked per plot or split-plot. Eggs and settled 1st instar nymphs were marked on separate leaves on separate plants. Cohorts were established on a single day, usually during morning hours.

2.2.2. Experimental treatments

To examine the effects of whitefly control regimes a total of six cohorts were established over a three year period to contrast plots treated or not for *B. tabaci*; 31 July and 11 August in 1997, 6 August and 1 September in 1998, and 9 and 31 August in 1999. These dates coincide with the initial application of whitefly insecticides and a period 2–4 weeks following the first applications in each year. Due to limitations in resources, these contrasts were restricted to sub-plots that that did not received any insecticide applications

for *L. hesperus* suppression. To further examine the indirect effects of *L. hesperus* suppression on whitefly mortality a total of eight cohorts were established over a three year period; 31 July in 1997, 17 July, 6 and 25 August and 25 September in 1998, and 26 July and 9 and 31 August in 1999. These dates coincided with the initial application of insecticides for *L. hesperus* and a period of 3–10 weeks following the first applications. Analyses were restricted to cohorts established in the two sub-plots of the whitefly untreated control main plots to eliminate any confounding effects of whitefly insecticides.

2.2.3. Determination of mortality factors

After cohorts were established, we examined each marked individual nymph every 2–3 days (3 times per week) in the field with the aid of a 15× Peak loupe (Light Impressions, Brea, CA, USA) until that individual died or emerged as an adult whitefly. We found that even with a 15× lens it was difficult to determine the fate of eggs, so we collected the leaves containing eggs after 8–10 days and examined them under a dissecting scope in the laboratory. Under typical temperatures during the summer months in central Arizona, eggs complete development in 5–7 days. On each observation date, we recorded the instar of each live nymph and the instar and cause of death of each dead nymph. Mortality was recorded as due to dislodgement, insecticides, predation, parasitism, inviability (eggs only), and unknown causes. Dislodgement could be caused by weather (wind and/or rain) or chewing predation, mainly from *Collops* spp. beetles [Coleoptera: Melyridae] and various lady beetles [Coleoptera: Coccinellidae]. The stadium of dislodged nymphs was estimated based on the average stage of other dead nymphs on the same observation date. Predation was mortality primarily due to sucking predators, which evacuated the contents of the whitefly body leaving only a deflated and transparent nymphal cuticle or egg chorion on the leaf. Prior analyses (Naranjo and Ellsworth, 2005) suggest sucking predation is primarily due to *Geocoris punctipes* (Say) [Hemiptera: Lygaeidae], *G. pallens* Stål [Hemiptera: Lygaeidae], *Orius tristicolor* (White) [Hemiptera: Anthocoridae], *Chrysoperla carnea* s.l. [Neuroptera: Chrysopidae] and the omnivore *L. hesperus*. On rare occasion the effects of chewing predation could be seen for nymphs (i.e., partial cadaver) or eggs (i.e., remnant of egg visible as pedicel still anchored in the leaf). Parasitism by *Eretmocerus* spp. and *Encarsia* spp. [Hymenoptera: Aphelinidae] could be distinguished by the displacement of mycetomes or the presence of parasitoid larvae or pupae within 4th instar hosts. Inviable eggs appeared normal, but failed to eclose. The nature of insecticide-induced death varied depending on the insecticide used. Buprofezin is a chitin synthesis inhibitor and its activity was apparent from otherwise intact nymphs that had discolored and/or distorted cuticles. Eggs are not affected by this compound. The juvenile hormone analog pyriproxyfen affects the terminal molt from the fourth stadium to the adult stage and also disrupts embryogenesis in the egg stage. Thus, mortality from this insecticide was apparent as egg inviability or intact fourth instar nymphs that were discolored and/or distorted or that failed to eclose after an extended period of time. The effects of conventional insecticides were apparent only in the nymphal stages where they caused discoloration and some distortion in intact nymphs.

To maintain uniformity in determining causes of death, only five people made all the field observations over the 3 years of the study and they frequently consulted one another throughout the study. Furthermore, a single observer in any given year made all determinations within a single replicate (block) of the experiment. A single observer determined causes of death for all eggs once they were returned to the laboratory. Once all the marked individuals on a leaf either died and/or emerged, the leaf was collected and returned to the laboratory to verify the cause of death with a dissecting microscope. Given our method of cohort establishment, we did not explicitly measure mortality of first instar crawlers. However, the duration between eclosion and settling averages less than 3–6 h (Price and Taborsky, 1992; Simmons, 2002) and greenhouse and field studies indicate that crawler mortality on cotton is negligible (Naranjo, 2007).

2.3. Insect density

Densities of *B. tabaci* eggs, nymphs, and adults were estimated each week from late June through late September or early October each year. Nymph and egg densities were estimated by the method of Naranjo and Flint (1994), which consists of counting individuals under a dissecting microscope on a 3.88 cm^2 disk taken from the fifth mainstem leaf below the terminal. Nymphs were categorized as either small (1st or 2nd instar) or large (3rd or 4th instar). The densities of adults were estimated by counting individuals, *in situ*, on the underside of leaves from the fifth mainstem node below the terminal (Naranjo and Flint, 1995). Ten to 30 sample units were randomly collected for immature and adult stages in each plot or split-plot on each sample date. Densities of *L. hesperus* were estimated each week with a standard 38-cm diameter sweep net from early June through late September each year. Two sets of 25 sweeps (50 total) were collected in each plot using a random starting point. Natural enemy populations were sampled as part of a companion study and are reported elsewhere (Naranjo et al., 2004).

2.4. Estimation of mortality rates

Standard methods (Southwood, 1978; Varley et al., 1973; Carey, 1993) were used to construct partial life tables of *B. tabaci* for each treatment plot and cohort. Four to five mortality factors affect each of the five immature developmental stadia of *B. tabaci* and they act in a contemporaneous fashion. That is, there is no obvious sequence of mortality agents affecting each stadium, thus, mortality from one agent might obscure the action of another. The concepts proposed by Royama (1981), and later elaborated by Buonaccorsi and Elkinton (1990) and Elkinton et al. (1992), were used to estimate stage-specific, marginal rates of mortality for each factor based on observed (i.e., apparent) stage-specific mortalities. The marginal rate estimates the level of mortality arising from a single factor as if that was the only factor operating. "Dislodgement" is the only mortality factor for which the apparent rate of death is equal to the marginal rate of death, because this cause of death cannot be obscured by any other contemporaneous factor. For all other mortality factors, marginal rates of death, M_B, were estimated from the general equations

$$M_B = d_B/(1 - cM_A), \tag{1}$$

$$M_A = (b - (b^2 - 4cd_A)^{0.5})/2c, \tag{2}$$

$$b = c(d_A + d_B) + 1 - d_B, \tag{3}$$

where A and B denote competing contemporaneous mortality factors, d_B is the apparent rate of mortality from factor B, d_A is the sum of apparent mortalities from all other relevant contemporaneous factors, c is an index that describes the outcome of competition between mortality factors A and B, and Eq. (2) is the quadratic solution for M_A. The probability that factor A obscures factor B is c while the probability that factor B obscures A is $1 - c$. For purposes here $c = 1$, because factor A, as defined, always obscures factor B when both affect the same insect. Thus, by algebraic manipulation Eq. (1) simplifies to

$$M_B = d_B/(1 - d_A). \tag{4}$$

Table 2 outlines the apparent rates of mortality needed to estimate marginal rates for each factor of interest within each developmental stadium of *B. tabaci* based on Eq. (4). Buonaccorsi and Elkinton (1990) showed that Eqs. (1)–(4) were approximate in cases when there was more than one interacting mortality factor. Further, the level of error is related to the probability that individuals are attacked by three or more agents. It was assumed that this probability was very low for *B. tabaci* given the short developmental periods of each life stage and the frequent observation intervals. Comparing measured generational mortality to that estimated from stage-specific, marginal death rates for the cohorts examined here resulted in an average error of 0.23%. For most subsequent analyses, mortalities were expressed as *k*-values ($k = -\ln[1 - M]$), where *M* is the marginal rate of mortality for a given factor during a given developmental stadia. The use of *k*-values is convenient, because they are additive across stages and mortality factors. *k*-values can be converted back into proportional mortality rates by $1 - e^{[-k]}$.

Because the insecticide pyriproxyfen causes egg inviability it was necessary to partition the amount of apparent mortality due to this insecticide from that due to inviability from other causes. Inviability in eggs was consistently observed in all treatment plots. The apparent level of inviability was averaged over all treatment plots within each replicate block excluding the pyriproxyfen plots. This value was then subtracted from the apparent rate of inviability in pyriproxyfen plots to arrive at an estimate of inviability due to this insecticide. Marginal mortality due to insecticide was then estimated from this corrected apparent rate using the equations above.

2.4.1. Key factor, density-dependence, and other statistical analyses

Key factor analysis was conducted using the method of Podoler and Rogers (1975) where individual *k*-values are regressed on total *K* (Σk). This method identifies the key factor as that associated with the largest regression coefficient (slope). Density-dependence of mortality factors was examined by regressing individual *k*-values on *ln* densities of the various life stages at the beginning of the generation. These densities were estimated from weekly sampling (see above) and linear interpolation was used as needed to provide density estimates on the date of cohort establishment. Because nymphs were classified as only small (instars 1 and 2) or large (instars 3 and 4) during sampling, we examined density-dependence for these nymphal groups by summing *k*-values over appropriate stages. Also, because insect densities (independent variables) are measured with error, we used ranged-major-axis regression analysis (Legendre, 2001) to quantify and test the strength of density-dependence. Sample permutation was used to determine if the slope of this relationship was different from zero (Legendre, 2001).

Mixed-model analysis of variance was used to test for differences in levels of marginal mortality from multiple factors due to whitefly management regimes within each post-treatment cohort. The block variable and associated interaction terms were entered as random effects, and Satterthwaite's formula was used to estimate corrected degrees of freedom for *F* tests. Tukey's adjustment to differences of least square means was used to separate treatment means (Littell et al., 1996). Similar analyses were used to test the effects of *L. hesperus* suppression on whitefly mortality factors from multiple cohorts in each year. Marginal mortality rates were transformed by arcsine $\sqrt{p}$ to normalize residuals and homogenize treatment variances. Mixed model, repeated-measures analysis of variance was used to test for treatment effects in seasonal densities of *B. tabaci* relative to whitefly and *L. hesperus* insecticides. Again, Tukey's adjustment to differences of least square means was used to separate treatment means.

Finally, the method of Carey (1989) was used to estimate irreplaceable mortality for individual mortality factors. The general form of this calculation is

$$\left(1 - \prod_{1}^{j}[1 - M_i]\right) - \left(1 - \prod_{1}^{j-1}[1 - M_i]\right), \tag{5}$$

where M_i is the marginal mortality rate for factor *i* over the total number of all mortality factors, *j*. The first product includes all mortality factors while the second product includes all mortality factors except the one for which irreplaceable mortality is being calculated. This method does not take into account any compensation that may occur if certain mortality agents act in a density-dependent manner.

3. Results

3.1. Whitefly mortality and population dynamics

Multiple mortality factors affected *B. tabaci* populations in all treatment plots following the first application of insecticides in 1997 (Fig. 1A). As expected, marginal rates of mortality from insecticides were high in all sprayed plots and significantly ($P < 0.05$) different from that observed in the untreated control. Mortality due to egg inviability and dislodgement were relatively high but did not differ among treatments. Mortality from natural enemies, primarily sucking predators, was relatively high, but significantly ($P < 0.05$) depressed in all insecticide regimes compared with the untreated control. Mortality from unknown sources was very low but did differ among treatments with higher levels in control plots and those treated with the IGR pyriproxyfen. Overall patterns of mortality changed considerably in cohorts observed 2–4 weeks after the initial application of insecticides (Fig. 1B). Insecticide-induced mortality declined in all treated plots and was statistically indistinguishable among plots receiving buprofezin or conventional materials or no sprays at all. Mortality from pyriproxyfen remained relatively high and significantly greater ($P < 0.05$) than all other treatments. Egg inviability was consistently low in all treatments; dislodgement was higher but equal in all

Table 2
Matrix for estimating marginal rates of mortality (M_B) from apparent rates of relevant competing contemporaneous factors using $M_B = d_B/(1 - d_A)$ for each defined developmental stage.

Stage	Marginal rate (M_B)	Apparent rate (d_B)	Apparent rate (d_A)
Egg, all nymphal stages	Insecticide	Insecticide	Predation + dislodgement
Egg	Inviability	Inviability	Predation + dislodgement
1st–4th stage nymphs[a]	Parasitism	Parasitism	Predation + dislodgement
Egg, all nymphal stages	Predation	Predation	Dislodgement
Egg, all nymphal stages	Unknown	Unknown	Predation + dislodgement
Egg, all nymphal stages	Dislodgement[b]	Dislodgement	

[a] Aphelinid parasitoids can successfully attack all nymphal stages of *B. tabaci* (Foltyn and Gerling, 1985; Headrick et al., 1995; Liu and Stansly, 1996), but can only be observed in 4th stage nymphs in the field; thus d_A is the sum of apparent predation and dislodgement from all nymphal stages combined.
[b] The apparent rate of dislodgement estimates the marginal rate directly.

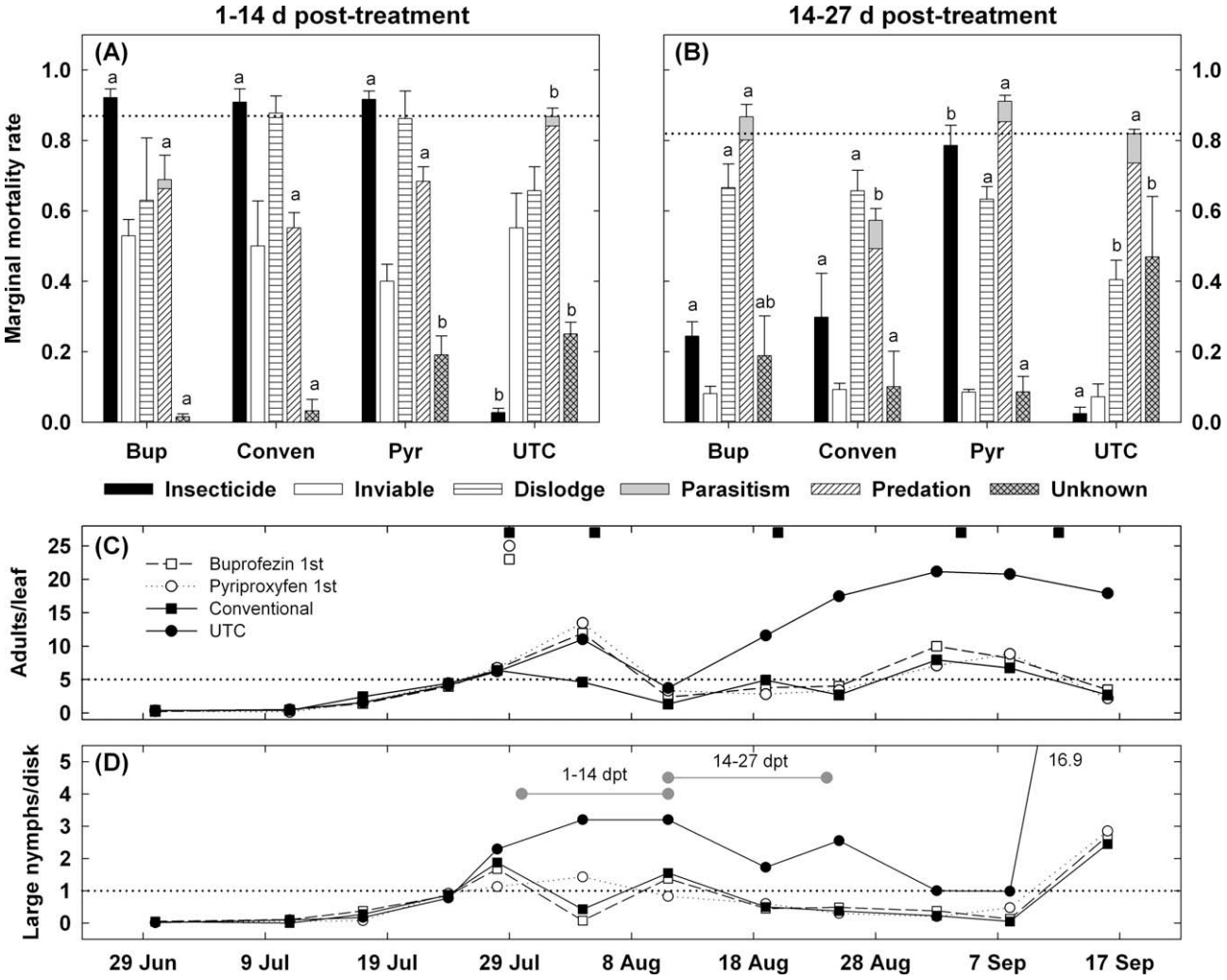

Fig. 1. (A and B) Marginal mortality rates for *B. tabaci* in cotton by various mortality factors pooled over all life stages in cohorts immediately following the first application of insecticides and 2–4 weeks later. Bars within a factor followed by different letters denote statistical significance ($P < 0.05$, Tukey test). Bars without letters did not differ among treatments. Error bars are SE ($n = 4$). The dotted lines indicate the base level of mortality from predation and parasitism combined in the untreated control. (C and D) Mean densities of adults and large nymphs (3rd and 4th instar) of *B. tabaci* over the season. Symbols along the top of each panel denote the timing of insecticide applications for each treatment and the dotted horizontal lines denote the dual economic threshold of 5 adults per leaf and 1 large nymph per leaf disk. The gray barbells indicate the timing of each life table cohort, 1997, Maricopa, AZ. Bup = buprofezin regime, Conven = conventional regime, Pyr = pyriproxyfen regime, UTC = untreated control.

insecticide-treated plots compared with the control ($P < 0.05$). Mortality from natural enemies, again primarily predators, rebounded to untreated control levels in the IGR regimes but remained significantly ($P < 0.05$) depressed in the broad-spectrum insecticide regime. Unknown mortality was generally low and variable with the highest level observed in control plots.

All insecticide treatments led to reductions in pest density below threshold levels for variable amounts of time relative to the control ($P < 0.05$) (Fig. 1C and D). Densities remained below threshold levels for nearly the rest of the season in plots treated with a single application of either IGR. In contrast, multiple applications of conventional, broad-spectrum materials were needed to achieve the same level of seasonal suppression. Populations in the untreated control generally increased as the season progressed and ended the season in outbreak status.

Similar overall patterns in mortality were observed following the first application of insecticides in 1998 (Fig. 2A) where high rates of insecticide mortality and low rates of natural enemy mortality, again primarily from sucking predators, were observed in treated plots compared with the control ($P < 0.05$). Levels of egg inviability were extremely high but did not differ ($P > 0.05$) among treatments. Likewise, mortality due to dislodgement and unknown causes did not vary significantly among treatments. In cohorts observed 4–6 weeks after insecticide applications, rates of insecticide mortality, egg inviability and dislodgement were low to moderate and did not differ among treatments (Fig. 2B). Rates of mortality from natural enemies again rebounded to control levels in the IGR regimes, but remained depressed in plots sprayed with broad-spectrum materials. This pattern occurred despite only a single application of any insecticides throughout the entire season.

Pest densities in all treated plots were significantly lower than the control ($P < 0.05$); however, even population densities in the control plots remained relatively low over the season. Densities of large nymphs only began to increase in late September (Fig. 2C and D). As noted, only a single application of any material applied in early August was required to suppress populations below the economic threshold throughout the season.

In the final year, mortality patterns seen in the two prior years were once again observed, but with a few exceptions (Fig. 3A). Following initial applications, insecticide mortality was high in all sprayed plots compared with the control and exceptionally high in plots treated with buprofezin. Mortality rates from natural

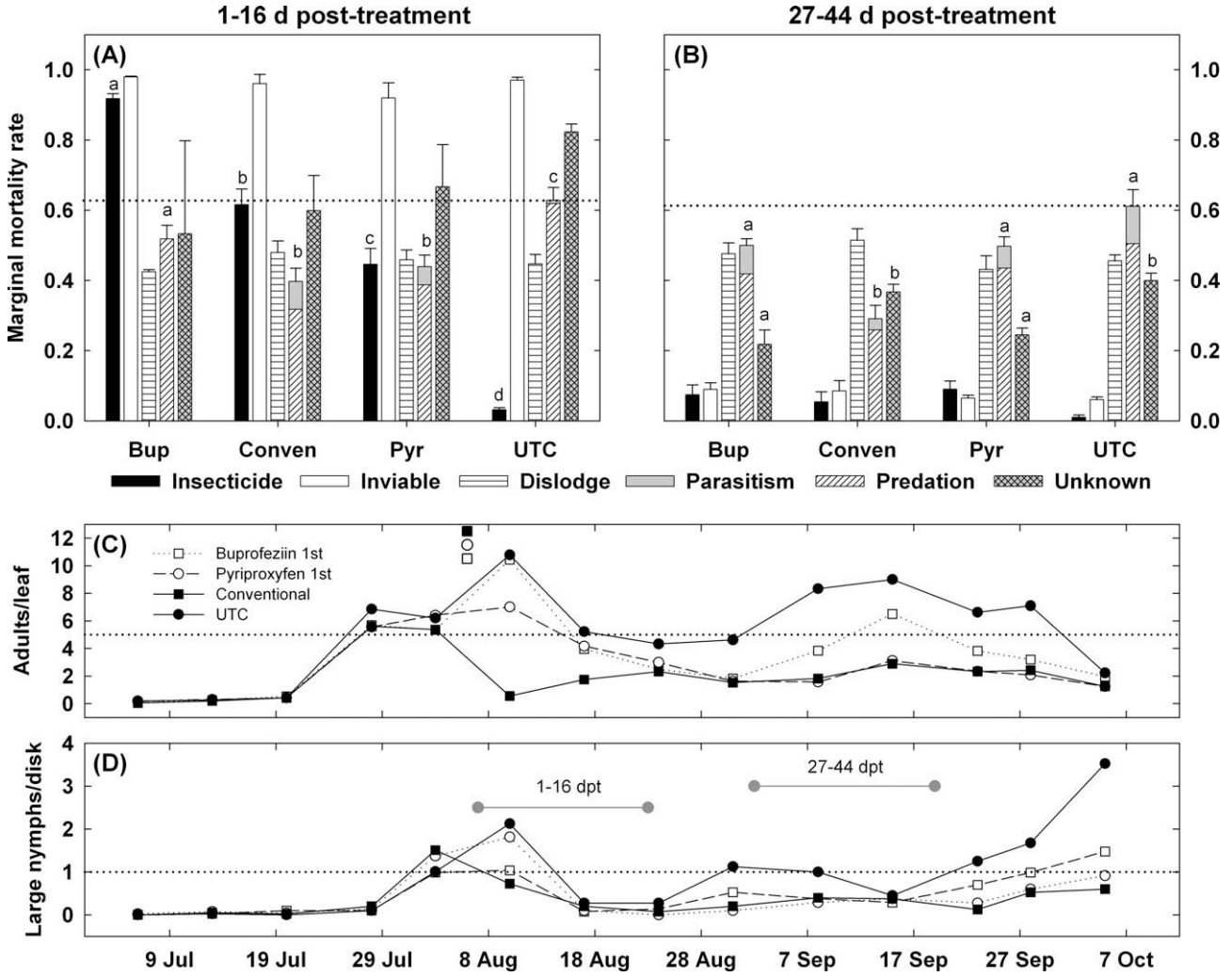

Fig. 2. (A and B) Marginal mortality rates for *B. tabaci* in cotton by various mortality factors pooled over all life stages in cohorts immediately following the first application of insecticides and 4–6 weeks later. Bars within a factor followed by different letters denote statistical significance ($P < 0.05$, Tukey test). Bars without letters did not differ among treatments. Error bars are SE ($n = 4$). The dotted lines indicate the base level of mortality from predation and parasitism combined in the untreated control. (C and D) Mean densities of adults and large nymphs (3rd and 4th instar) of *B. tabaci* over the season. Symbols along the top of each panel denote the timing of insecticide applications for each treatment and the dotted horizontal lines denote the dual economic threshold of 5 adults per leaf and 1 large nymph per leaf disk. The gray barbells indicate the timing of each life table cohort, 1998, Maricopa, AZ. Bup = buprofezin regime, Conven = conventional regime, Pyr = pyriproxyfen regime, UTC = untreated control.

enemies, mainly sucking predators, were significantly ($P < 0.05$) depressed in plots receiving pyriproxyfen or conventional materials compared with the control. Levels of predation in the buprofezin regime equaled that in the control. Rates of egg inviability and dislodgement were moderate and did not differ among treatments ($P > 0.05$). However, high levels of unknown mortality were observed in all plots but those treated with buprofezin. Three to five weeks following sprays, rates of mortality from insecticides declined but were higher than rates observed in the control. Once again, mortality from natural enemies remained steady or rebounded in the plots sprayed with buprofezin or pyriproxyfen, respectively while that in plots sprayed with broad-spectrum materials remained significantly ($P < 0.05$) depressed (Fig. 3B). Unknown mortality was moderate and variable among treatments.

Insecticide applications effectively suppressed populations of *B. tabaci* below economic levels relative to the control ($P < 0.05$). This control was achieved with either a single application of either IGR or three applications of conventional insecticides (Fig. 3C and D). Populations in control plots increased over the season and declined on their own naturally beginning in late September.

3.2. Influence of control for L. hesperus

The application of broad-spectrum insecticides for the suppression of *L. hesperus* generally had a significant effect on insecticide and natural enemy-induced mortality of *B. tabaci* but not on other mortality factors (Fig. 4A). In five out of 8 cohorts, insecticides applied for *L. hesperus* led to significantly ($P < 0.05$) higher rates of insecticide mortality in *B. tabaci*. However, in nearly all cohorts observed (7 of 8) rates of mortality from natural enemies were significantly ($P < 0.05$) depressed by these applications. Despite these patterns, population densities of *B. tabaci* in sub-plots treated or not for *L. hesperus* were generally unaffected over extended portions of the season in each year (Fig. 4B; $P > 0.05$).

3.3. Key factors

For *B. tabaci* cohorts that were observed immediately following the initial application of insecticides, the key factor (largest regression coefficient) was insecticides in all treated plots (Fig. 5). The key factor in the untreated control was predation. In cohorts observed 2–6 weeks later, predation was the key factor in the

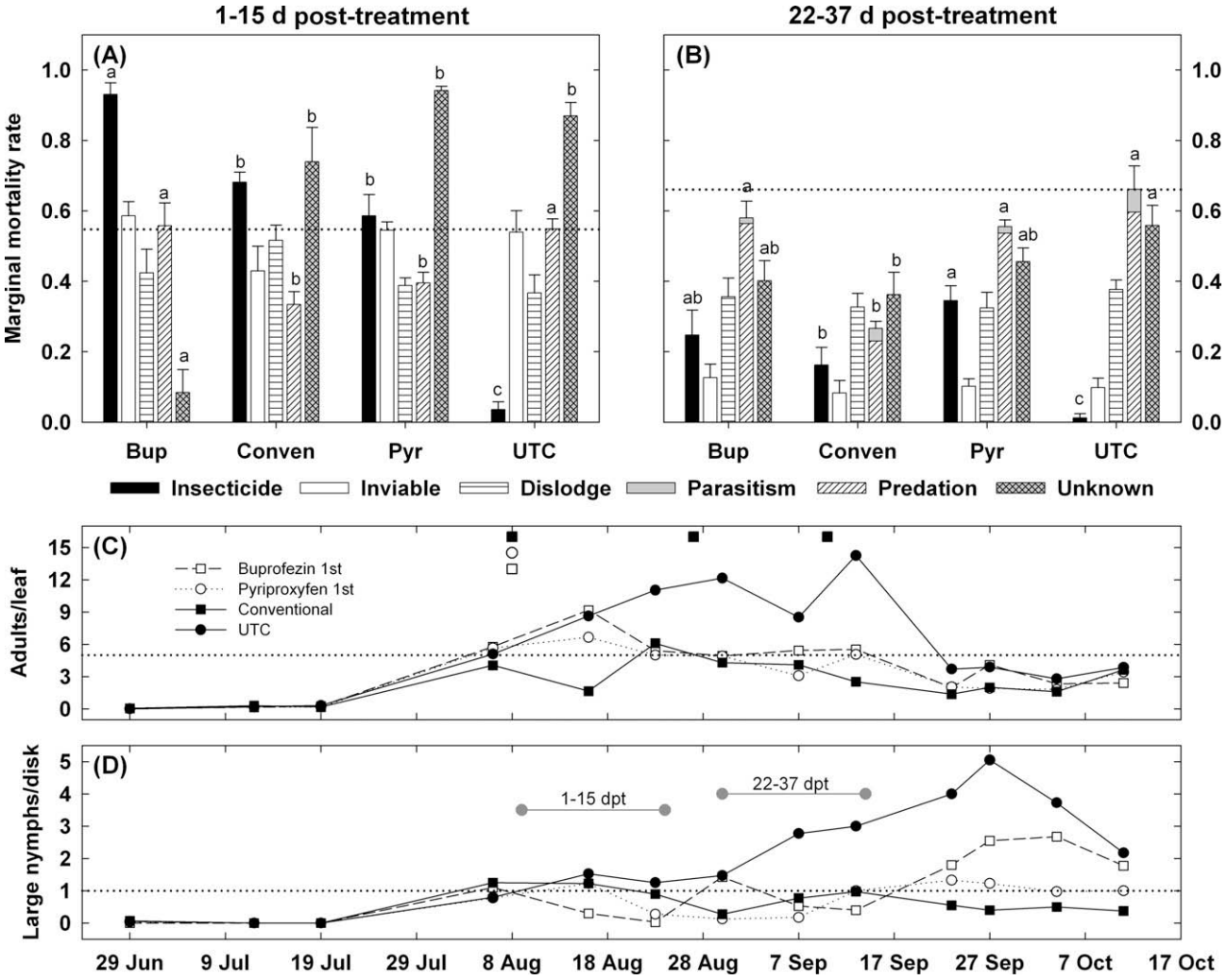

Fig. 3. (A and B) Marginal mortality rates for *B. tabaci* in cotton by various mortality factors pooled over all life stages in cohorts immediately following the first application of insecticides and 3–5 weeks later. Bars within a factor followed by different letters denote statistical significance ($P < 0.05$, Tukey test) Bars without letters did not differ among treatments. Error bars are SE ($n = 4$). The dotted lines indicate the base level of mortality from predation and parasitism combined in the untreated control. (C and D) Mean densities of adults and large nymphs (3rd and 4th instar) of *B. tabaci* over the season. Symbols along the top of each panel denote the timing of insecticide applications for each treatment and the dotted horizontal lines denote the dual economic threshold of 5 adults per leaf and 1 large nymph per leaf disk. The gray barbells indicate the timing of each life table cohort, 1999, Maricopa, AZ. Bup = buprofezin regime, Conven = conventional regime, Pyr = pyriproxyfen regime, UTC = untreated control.

IGR regimes and again in the untreated control. For cohorts observed in the broad-spectrum insecticide regime, the key factor was dislodgement followed closely by insecticides.

3.4. Irreplaceable mortality

An additional means of quantifying the relative importance of mortality factors is to calculate the irreplaceable or indispensable mortality contributed by each factor. Irreplaceable mortality was estimated as the difference between the total level of mortality from all factors, and that based on all mortality minus the factor of interest. Because mortality from either predation or insecticides appeared to be most important in terms of understanding pest dynamics (see Figs. 1–3 and 5) and because irreplaceable mortality was consistently low for all other factors, only analyses for these two factors are shown (Fig. 6). In cohorts observed immediately following insecticide applications, the highest levels of irreplaceable mortality (≈5–6%) were due to insecticides in all treated plots. Predation supplied the highest level of irreplaceable mortality (≈8%) in the untreated control plots. In the period 2–6 weeks later, irreplaceable mortality from insecticides declined to about 2–4% in treated plots while irreplaceable mortality from predation increased dramatically in all plots. The lowest level of irreplaceable mortality from predation was observed in the broad-spectrum insecticide treatment (≈5%), with that in the IGR regimes averaging over 10%.

3.5. Density-dependence of mortality factors

Overall, little density-dependence in mortality was observed under any treatment regime, and density-dependence was weak in most of the instances in which it was observed (Table 3). No density-dependent mortality was observed in any cohorts established immediately before the initial application of insecticides. Positive density-dependence was observed in egg and large nymph predation and in dislodgement (presumably from chewing predation) of small nymphs from the buprofezin regime 2–6 weeks after application. Likewise, density-dependent predation was observed for eggs and large nymphs in pyriproxyfen-treated plots 2–6 weeks following application. Positive density-dependence also was observed in dislodgement, most likely through the action of chewing predators, and parasitism of large nymphs in these treatment plots,

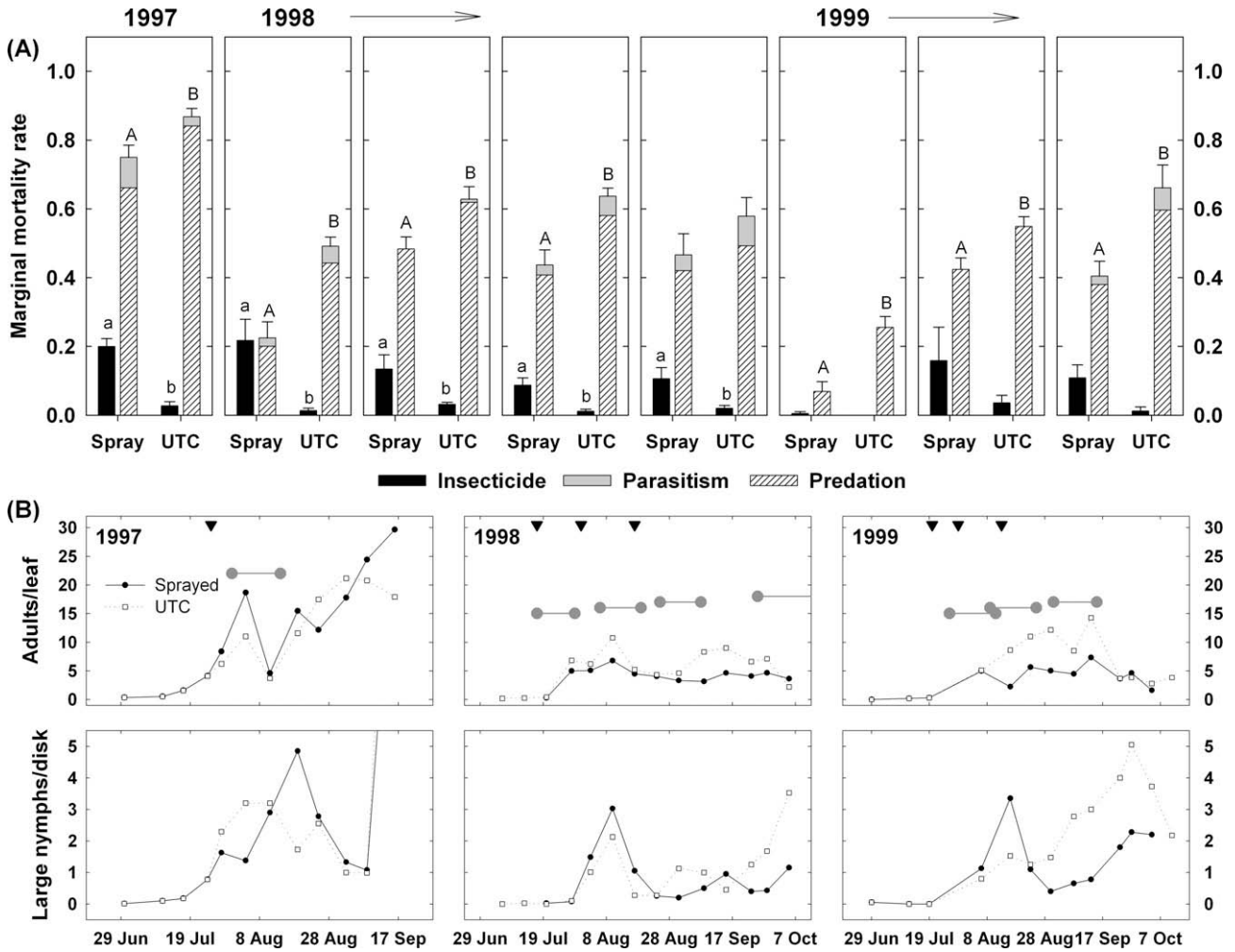

Fig. 4. (A) Contrast of marginal mortality rates for *B. tabaci* in cotton from insecticides and natural enemies, pooled over all life stages, between sub-plots sprayed or not sprayed for *L. hesperus*. Bars within a factor followed by different letters denote statistical significance ($P < 0.05$, Tukey test). Bars without letters did not differ between treatments. Rates of mortality due to other factors did not differ between treatments and are not presented. Error bars are SE ($n = 4$). (B) Mean densities of adults and large nymphs (3rd and 4th instar) of *B. tabaci* over the season. Triangles along the top of each panel denote the timing of insecticide applications for *L. hesperus*. The gray barbells denote the timing of each life table cohort, 1997–1999, Maricopa, AZ.

with the strength of the latter being relatively high. No density-dependence was observed in the broad-spectrum insecticide regimes and only dislodgement of eggs was weakly density-dependent in the untreated control (Table 3).

4. Discussion

Conservation biological control is warranted when natural enemies contribute in a tangible way to the suppression of one or more pests in the system (Greathead, 1995). Life table studies in untreated cotton (Naranjo and Ellsworth, 2005) revealed that predation is an important factor in population regulation of *B. tabaci*, though insufficient on its own to prevent economically damaging levels of *B. tabaci* in Arizona cotton. The IGRs buprofezin and pyriproxyfen are selective relative to more conventional alternatives (Naranjo et al., 2003, 2004). On a seasonal basis, population densities of 20 arthropod predators declined just 7% on average over a three year period when either IGR was used compared with an average reduction of 32% when broad-spectrum insecticides were used (Naranjo et al., 2004). Predator conservation combined with excellent short-term insecticide efficacy led to higher and more favorable predator to prey ratios in IGR regimes (Naranjo et al., 2004). Our life table results here quantitatively demonstrate that this conservation can tangibly effect pest suppression and help drive integrated control in this system.

Bemisia tabaci populations in Arizona cotton proceed through periods of very low densities ostensibly under natural control to exponential increase fueled in part by immigration and then decline due to natural control and emigration. They can be found in very low numbers on cotton plants relatively soon after the plant emerges and early season population growth is slow due in part to natural mortality forces, cooler weather, and other biological factors (Naranjo and Ellsworth, 2005; see simulations in Crowder et al., 2006). *B. tabaci* is polyphagous, has no diapause, and readily moves among and reproduces on a wide variety of cultivated and wild host plants in the southwestern USA (Watson et al., 1992). In central Arizona, populations of *B. tabaci* build in spring-planted cantaloupe and then migrate in mass to host plants such as cotton in early to mid-summer (unpublished data). Simulation studies have shown that this migration overwhelms the growth of resident populations present in cotton and leads to rapid population growth, typically in July (Naranjo and Ellsworth, 2005). Even though immature *B. tabaci* are subject to high levels of natural mortality (median 93.4%) in unsprayed cotton (Naranjo and Ellsworth, 2005) this mortality is insufficient to maintain populations below economically damaging levels in most years. The capacity of

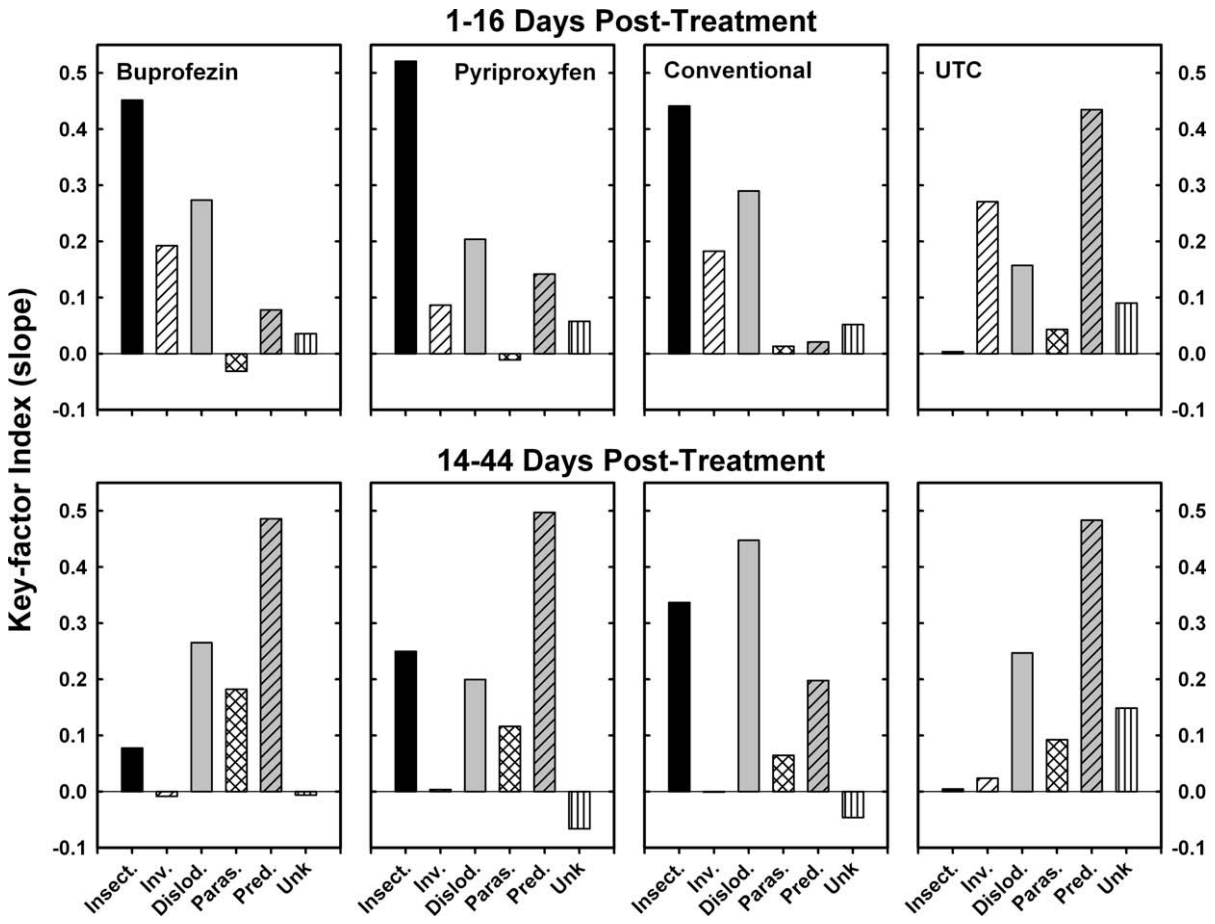

Fig. 5. Key factor analyses of life tables over all three years relative to the initial application of insecticides for *B. tabaci* control, Maricopa, AZ. Analyses examined each factor pooled over all life stages. The key factor index represents the slope of the regression (n = 12) of factor k-values on total K-values (Σk) with the largest slope indicating the key factor (see Podoler and Rogers, 1975).

natural mortality forces, particularly natural enemies, to regulate populations is overwhelmed and insecticides are needed to suppress further population increase.

Through quantitative measurement and contrast of control dynamics in the *B. tabaci*/cotton system, we identify the optimal deployment of chemical and biological control tactics. The result is a more stable system of integrated control (*sensu* Stern et al., 1959) such that selective insecticides and conserved beneficial arthropods augment each other's control potential. The use of insecticides, whether broad-spectrum or selective, was associated with season-long pest control; however, the manner in which this suppression was manifested and the underlying mechanisms leading to suppression was dependent on the type of insecticide used and its impact on conservation biological control. The use of insecticides when the economic threshold was first reached results in initial pest suppression, and life table analyses confirmed insecticide mortality as the key factor for that generation. This is consistent with the known efficacy and temporal action of these materials (Ellsworth and Naranjo, 1999; Naranjo et al., 2004). Insecticides added a small but irreplaceable amount of mortality essential for pest suppression in all treatment regimes and primarily replaced that provided by predators during this initial time period. However, in subsequent generations established 2–6 weeks later, natural enemy-induced mortality returned to the high levels observed in the unsprayed control and assumed the role of key factor in regimes based on selective IGRs. In contrast, regimes based on broad-spectrum insecticides continued to show significantly lower mortality by natural enemies. A single application of either IGR was sufficient to suppress *B. tabaci* populations throughout much of the growing season while as many as five applications of broad-spectrum compounds were needed to achieve similar levels of season-long control.

Some insecticide-induced mortality was observed beyond the initial period (>2 weeks) but at much reduced levels compared with that observed immediately following sprays. Nevertheless, pest populations remained low suggesting conserved natural enemies play a key role, perhaps along with other natural forces like weather, where selective insecticides were used. This effect has been coined the "bioresidual" (Ellsworth and Martinez-Carrillo, 2001; Naranjo, 2001) and represents the combined contribution of all natural mortality factors, with particular emphasis on biological control, that allow for a lowering of the general equilibrium position of the target pest and long-term pest control following the use of selective insecticides. The important contribution of arthropod predators is bolstered by evidence of density-dependence, albeit weak, in predation on eggs and large nymphs in the IGR regimes and the high levels of irreplaceable mortality provided by predation in later generations of *B. tabaci*. Naranjo and Ellsworth (2005) showed that the highest overall levels of mortality occur during the 4th nymphal stadium and then during the egg stage in untreated cotton. Thus, even weak levels of positive density-dependence in these stages, as shown here, may limit population growth and contribute to the "bioresidual" effect that augments pest control.

Insecticides are frequently used in pest management systems and are often viewed as the control component inflicting the most

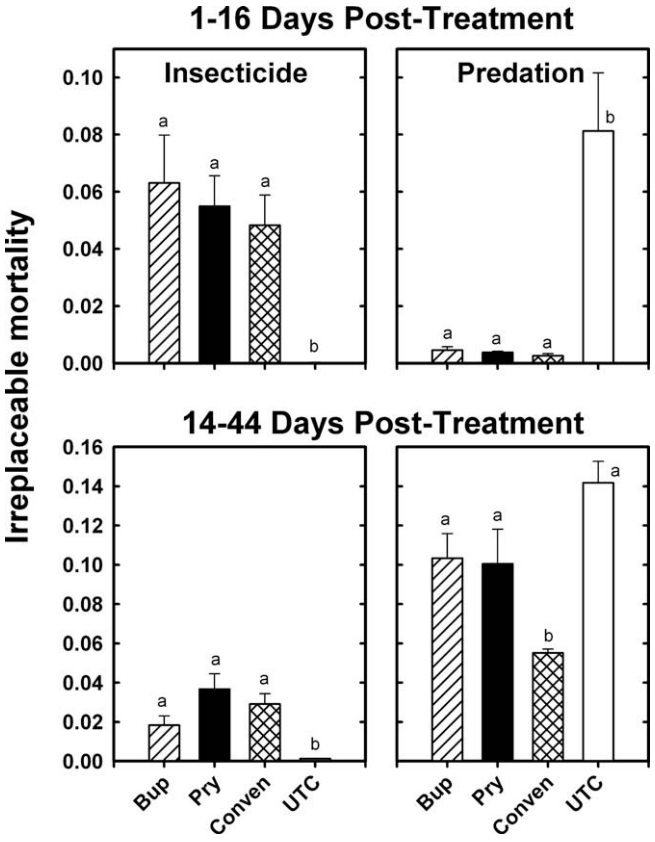

Fig. 6. Estimates of irreplaceable mortality provided by insecticides and predation for each treatment regime relative to the initial application of insecticides for *B. tabaci* control, Maricopa, AZ, 1997–1999. Error bars are SE (n = 12).

pest mortality. Standard measures of insecticide efficacy are used to benchmark, compare and recommend compounds for use by growers. However, as Waage (1989) notes, the actual effect of an insecticide may be substantially less than expected when one considers the interaction of insecticides and natural enemies. Such is the case here where life table analyses enabled us to measure marginal rates of mortality, and perhaps more importantly, to estimate the irreplaceable mortality provided by insecticides. Marginal rates of mortality from insecticides ranged from ≈40–90% in the generation present at the time of insecticide treatment. In contrast, the irreplaceable (and essential) mortality supplied by insecticides at this time was estimated at only 5–6%. Much of the marginal insecticide mortality came at the expense of that supplied by natural enemies and is reflected in the low levels of irreplaceable mortality from natural enemies during this same time period (<0.5%; see Fig. 6). In turn, the irreplaceable mortality (ca. 10%) supplied by predators later in the season one or more generations after selective insecticides are used is key to the season-long lowering of the general equilibrium position and the pest suppression observed. Such tradeoffs between insecticides and biological control in terms of pest mortality likely play out in many agricultural systems as predicted by Stern et al. (1959), but only become apparent when precise *in situ* rates of death are categorized and estimated.

Cotton in most areas of the world is plagued by multiple pests. In Arizona, there are three key pests; *B. tabaci*, *L. hesperus* and *Pectinophora gossypiella* (Saunders) [Lepidoptera: Gelechiidae]. The latter pest is effectively controlled by the broad-scale use of selective transgenic Bt cotton (Carrière et al., 2003; Naranjo, 2005), currently at >98% adoption (Ellsworth et al., 2007). Bt cotton eliminates the need for insecticides to control this pest and was used in our study system. However, at the time of our study no effective selective options were available for suppression of *L. hesperus* and several sprays of broad-spectrum insecticides were applied for this pest in most years. Although we found that these sprays did not consistently alter seasonal populations of *B. tabaci*, small amounts of insecticide-induced mortality were recorded in life tables (see Fig. 4). These applications negatively affected rates of *B. tabaci* mortality from natural enemies in most instances, but surprisingly did not alter pest population dynamics in a consistent manner. We have consistently observed resurgence of *B. tabaci* in experiments examining *L. hesperus* control options over the past few years (Ellsworth and Naranjo, unpublished data; Asiimwe, Ellsworth and Naranjo, unpublished data). Here however, the differences in natural enemy-induced mortality, although significant, were relatively small in relation to the changes observed in *B. tabaci* management regimes (see Figs. 1–3) and in addition were probably largely offset by similarly small, yet increased levels of insecticide-induced mortality.

Table 3
Density-dependent analyses of mortality factors affecting various life stages of *B. tabaci* relative to cotton management regime, 1997–1999, Maricopa, AZ[a].

Stage/factor	Buprofezin 1st		Pyriproxyfen 1st		Conventional		Untreated control	
	1-16d post[b]	14-44d post	1-16d post	14-44d post	1-16d post	14-44d post	1-16d post	14-44d post
Egg								
Insecticide	NA	NA	−1.04 (0.30)	0.09 (0.15)	NA	NA	NA	NA
Inviability	0.07 (0.35)	0.01 (0.49)	0.83 (0.08)	0.02 (0.09)	0.26 (0.32)	0.19 (0.35)	0.92 (0.10)	0.04 (0.09)
Dislodgement	0.15 (0.20)	−0.48 (0.39)	0.25 (0.07)	−0.09 (0.12)	0.23 (0.07)	−0.31 (0.17)	0.13 (0.43)	**0.05 (0.01)**
Predation	−0.34 (0.19)	**0.23 (0.002)**	−0.23 (0.08)	**0.09 (0.02)**	0.38 (0.43)	0.20 (0.29)	0.47 (0.36)	0.15 (0.10)
Small nymph[c]								
Insecticide	−0.66 (0.35)	−0.14 (0.30)	0.06 (0.34)	−0.04 (0.27)	−0.52 (0.21)	0.05 (0.14)	0.03 (0.26)	−0.01 (0.45)
Dislodgement	−0.39 (0.16)	**0.17 (0.02)**	0.03 (0.43)	0.14 (0.06)	−0.16 (0.17)	0.12 (0.18)	0.06 (0.23)	0.05 (0.11)
Predation	−0.41 (0.12)	−0.09 (0.46)	0.06 (0.42)	−0.34 (0.46)	0.02 (0.49)	−0.02 (0.22)	−0.04 (0.52)	−0.12 (0.32)
Unknown	0.08 (0.20)	−0.11 (0.15)	0.08 (0.18)	0.14 (0.36)	−0.12 (0.39)	−0.06 (0.26)	0.08 (0.14)	−0.21 (0.20)
Large nymph[d]								
Insecticide	−0.49 (0.46)	0.12 (0.10)	0.65 (0.37)	0.82 (0.27)	0.56 (0.10)	0.23 (0.18)	−0.06 (0.30)	0.02 (0.62)
Dislodgement	−0.71 (0.22)	0.18 (0.11)	−1.31 (0.12)	**0.22 (0.02)**	0.42 (0.26)	0.15 (0.07)	−0.37 (0.41)	−0.12 (0.24)
Parasitism	0.33 (0.16)	0.30 (0.22)	0.18 (0.27)	**0.66 (0.02)**	−0.14 (0.19)	0.16 (0.15)	0.34 (0.16)	0.28 (0.09)
Predation	−0.75 (0.25)	**0.38 (0.05)**	−0.25 (0.11)	**0.19 (0.02)**	−0.06 (0.39)	0.17 (0.39)	0.76 (0.10)	0.29 (0.11)
Unknown	0.13 (0.28)	−0.59 (0.32)	0.21 (0.22)	−0.33 (0.13)	0.13 (0.13)	−0.19 (0.16)	−0.23 (0.19)	0.07 (0.38)

[a] Values represent the slopes (P-values) from ranged major-axis regression (Legendre, 2001); P value tests if slope >0 determined by 500 random permutations, n = 12. Bold values highlight those where $P < 0.05$).
[b] Range of time after the first application of insecticides for *B. tabaci* control.
[c] Combined 1st and 2nd instar *B. tabaci*.
[d] Combined 3rd and 4th instar *B. tabaci*.

The four key components of integrated control are sampling, thresholds, biological control and the use of physiologically or ecologically-based insecticide selectivity (Stern et al., 1959). Several or more of these basic components have been demonstrated in agricultural systems worldwide (e.g., van den Bosch and Stern, 1962; Hoyt and Burts, 1974; Collyer and van Geldermalsen, 1975; Zalom et al., 1984, 2001; Trumble and Morse, 1993; Settle et al., 1996; Furlong et al. 2004; Musser et al., 2006) but few studies have examined and quantified the mechanisms underlying the control dynamics of a system (also see Naranjo and Ellsworth, 2009). Life table analyses allowed us to categorize, quantify and interpret the effects of multiple mortality factors within the context of alternative management scenarios. Using life tables within an experimental approach (Bellows and Van Driesche, 1999) overcomes many of the limitations of life table analyses that are often criticized as insufficient to identify the factors causing population change (e.g., Royama, 1996). Clearly, the differential impact of selective and non-selective insecticides on natural enemy populations and the associated mortality they inflict on pest populations played a crucial role in control dynamics here and probably do so in many other agricultural systems. Since the implementation of a management program for *B. tabaci* based on prescriptive insecticide use and specific emphasis on conservation of natural enemies, overall insecticide use has declined from a decades high 12.5 applications per acre in 1995 (6.6 targeting *B. tabaci* directly) to often less than 3 applications per acre (0.4–2.0 targeting *B. tabaci* directly) throughout most of the past 10 years (Ellsworth et al., 2007). The IGRs used here along with one newer selective insecticide (i.e., moderate rates of spiromesifen) continue to be recommended to and used by growers for whitefly management in cotton (Ellsworth et al., 2006). Biological control plays a key role in the management of *B. tabaci* in our system and others, but our approach to understanding interacting mortality forces within a pest management context should be useful for identifying the combination of tactics, biological or otherwise, that are needed to effect efficient and sustainable management of pests in many other agricultural systems. Understanding interacting mortality forces through life tables also could push forward the development of economic thresholds that take into account natural enemy densities (e.g., Hoffmann et al., 1990; Giles et al., 2003; Hamilton et al., 2004; Conway et al., 2006; Musser et al., 2006) and the associated mortality they induce in pest populations, leading to an even greater integration of biological control in pest management systems.

Our detailed study of the Arizona cotton pest management system has revealed a rare, documented example of the Integrated Control Concept (Stern et al., 1959; also see Naranjo and Ellsworth, 2009). Naranjo and Ellsworth (2009) detailed the de novo development of rapid, easy to implement sampling plans and stage-based thresholds for preventing economic loss by *B. tabaci* in cotton. Here, we provide evidence for the final two components of integrated control, selective chemical controls that enable conservation biological control, with both augmenting the control system in concert. Naranjo and Ellsworth (2009) identified five postulates for demonstrating and validating operational integrated control. Our current study provides direct evidence for three of these: (1) biological control agents are able to survive, at some level, the application of selective controls in our system; (2) conservation biological control is functioning and produces irreplaceable mortality crucial to the control system; and (3) when the selective IGRs are used, an extended suppressive interval or bioresidual occurs that is in excess of what the chemical control itself can provide. Together with previous studies (see Naranjo and Ellsworth, 2009), the current study completes our validation of integrated control. This comprehensive examination of our control system helps bolster efforts to renew interest and confidence in biological control among producers and pest management practitioners, especially when specifically integrated with selective chemical controls.

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References

Abdelrahman, A.A., Munir, B., 1989. Sudanese experience in integrated pest management of cotton. Insect Science and Its Application 10, 787–794.

Asiimwe, P., Ecaat, J.S., Otim, M., Gerling, D., Kyamanywa, S., Legg, J.P., 2006. Life table analysis of mortality factors affecting populations of *Bemisia tabaci* on cassava in Uganda. Entomologia Experimentalis et Applicata 122, 37–44.

Bellows Jr., T.S., van Driesche, R.G., 1999. Life table construction and analysis for evaluating biological control agents. In: Bellows, T.S., Fisher, T.W. (Eds.), Handbook of Biological Control. Academic Press, San Diego, CA, pp. 199–223.

Bellows Jr., T.S., van Driesche, R.G., Elkinton, J.S., 1992. Life-table construction and analysis in the evaluation of natural enemies. Annual Review of Entomology 37, 587–614.

Breene, R.G., Dean, D.A., Quarles, W., 1994. Predators of sweetpotato whitefly. IPM Practitioner 16, 1–8.

Buonaccorsi, J.P., Elkinton, J.S., 1990. Estimation of contemporaneous mortality factors. Researches on Population Ecology 32, 151–171.

Carey, J.R., 1989. The multiple decrement life table: a unifying framework for cause-of-death analysis in ecology. Oecologia 78, 131–137.

Carey, J.R., 1993. Applied Demography for Biologist: With Special Emphasis on Insects. Oxford University Press, New York.

Carrière, Y., Ellers-Kirk, C., Sisterson, M., Antilla, L., Whitlow, M., Dennehy, T.J., Tabashnik, B.E., 2003. Long-term regional suppression of pink bollworm by *Bacillus thuringiensis* cotton. Proceedings of the National Academy of Sciences 100, 1519–1523.

Collyer, E., van Geldermalsen, M., 1975. Integrated control of apple pests in New Zealand 1. Outline of experiment and general results. New Zealand Journal of Zoology 2, 101–134.

Conway, H.E., Steinkraus, D.C., Ruberson, J.R., Kring, T.J., 2006. Experimental treatment threshold for the cotton aphid (Homoptera: Aphididae) using natural enemies in Arkansas cotton. Journal of Entomological Science 41, 361–373.

Croft, B.A., 1990. Arthropod Biological Control Agents and Pesticides. John Wiley and Sons, New York.

Crowder, D.W., Carriere, Y., Tabashnik, B.E., Ellsworth, P.C., Dennehy, T.J., 2006. Modeling evolution of resistance to pyriproxyfen by the sweetpotato whitefly (Homoptera: Aleyrodidae). Journal of Economic Entomology 99, 1396–1406.

DeBach, P., 1974. Biological Control by Natural Enemies. Cambridge Univ. Press, London.

DeBach, P., Hagen, K.S., 1964. Manipulation of entomophagous species. In: DeBach, P. (Ed.), Biological Control of Insect Pests and Weeds. Reinhold, New York, pp. 429–458.

Devine, G.J., Ishaaya, I., Horowitz, A.R., Denholm, I., 1998. Effects of piperonyl butoxide on *Bemisia tabaci* Genn. (Homoptera: Aleyrodidae): mortality, development, parasitism and predation in Israeli cotton fields. Crop Protection 17, 717–726.

Ehler, L.E., 1998. Conservation biological control: past, present, and future. In: Barbosa, P. (Ed.), Conservation Biological Control. Academic Press, New York, pp. 1–8.

Elkinton, J.S., Buonaccorsi, J.P., Bellows, T.S., Van Driesche, R.G., 1992. Marginal attack rate, *k*-values and density dependence in the analysis of contemporaneous mortality factors. Researches on Population Ecology 34, 29–44.

Ellsworth, P., Diehl, J., Dennehy, T., Naranjo, S., 1995. Sampling Sweetpotato Whiteflies in Cotton. IPM Series No. 2. Cooperative Extension, University of Arizona, Tucson (revised).

Ellsworth, P.C., Diehl, J.W., Naranjo, S.E., 1996. Sampling Sweetpotato Whitefly Nymphs in Cotton. IPM Series No. 6. Cooperative Extension, University of Arizona, Tucson.

Ellsworth, P.C., Fournier, A., Smith, T.D., 2007. Arizona Cotton Insect Losses. Publ. No. AZ1183 (rev. 9/08). University of Arizona, Cooperative Extension, Tucson, Arizona. Available from: <cals.arizona.edu/crops/cotton/insects/cil/cil.html>.

Ellsworth, P.C., Jones, J.S., 2001. Cotton IPM in Arizona: a decade of research, implementation & education. In: Dugger, P., Richter, D. (Eds.), Proceedings Beltwide Cotton Conferences. National Cotton Council, Memphis, TN, pp. 1088–1096.

Ellsworth, P.C., Martinez-Carrillo, J.L., 2001. IPM for *Bemisia tabaci*: a case study from North America. Crop Protection 20, 853–869.

Ellsworth, P.C., Naranjo, S.E., 1999. Whitefly management with insect growth regulators and the influence of *Lygus* controls. In: Cotton, A College of Agriculture Report. Series P-116. University of Arizona, Tucson, pp. 339–354.

Ellsworth, P.C., Palumbo, J.C., Naranjo, S.E., Dennehy, T.J., Nichols, R.L., 2006. Whitefly Management in Arizona Cotton 2006. Cooperative Extension. IPM Series No. 18. The University of Arizona, Tucson. Available from: <cals.arizona.edu/pubs/insects/az1404.pdf>.

Foltyn, S., Gerling, D., 1985. The parasitoids of the aleyrodid *Bemisia tabaci* in Israel: development, host preference and discrimination of the aphelinid wasp *Eretmocerus mundus*. Entomologia Experimentalis et Applicata 38, 255–260.

Furlong, M.J., Shi, Z.H., Liu, S.S., Zalucki, M.P., 2004. Evaluation of the impact of natural enemies on *Plutella xylostella* L. (Lepidoptera: Yponomeutidae) populations on commercial *Brassica* farms. Agricultural and Forest Entomology 6, 311–322.

Gerling, D., Alomar, O., Arnó, J., 2001. Biological control of *Bemisia tabaci* using predators and parasitoids. Crop Protection 20, 779–799.

Giles, K.L., Jones, D.B., Royer, T.A., Elliott, N.C., Kindler, S.D., 2003. Development of a sampling plan in winter wheat that estimates cereal aphid parasitism levels and predicts population suppression. Journal of Economic Entomology 96, 975–982.

Greathead, D.J., 1995. Natural enemies in combination with pesticides for integrated pest management. In: Reuveni, R. (Ed.), Novel Approaches to Integrated Pest Management. CRC Press, Boca Raton, FL, pp. 183–197.

Gurr, G.M., Wratten, S.D., 1999. 'Integrated biological control': a proposal for enhancing success in biological control. International Journal of Pest Management 45, 81–84.

Hamilton, A.J., Schellhorn, N.A., Endersby, N.M., Ridland, P.M., Ward, S.A., 2004. A dynamic binomial sequential sampling plan for *Plutella xylostella* (Lepidoptera: Plutellidae) on broccoli and cauliflower in Australia. Journal of Economic Entomology 97, 127–135.

Headrick, D.H., Bellows, T.S., Perring, T.M., 1995. Behaviors of female *Eretmocerus* sp nr *californicus* (Hymenoptera: Aphelinidae) attacking *Bemisia argentifolii* (Homoptera: Aleyrodidae) on sweet potato. Environmental Entomology 24, 412–422.

Hector, D.J., Hodkinson, I.D., 1989. Stickiness in cotton. In: ICAC Review Articles on Cotton Production Research No. 2. International Cotton Advisory Committee, Washington, DC.

Hoffmann, M.P., Wilson, L.T., Zalom, F.G., Hilton, R.J., 1990. Parasitism of *Heliothis zea* (Lepidoptera: Noctuidae) eggs: effect on pest management decision rules for processing tomatoes in the Sacramento Valley of California. Environmental Entomology 19, 753–763.

Horowitz, A.R., Ellsworth, P.C., Ishaaya, I., 2009. Biorational pest control — An overview. In: Ishaaya, I., Horowitz, A.R. (Eds.), Biorational Control of Arthropod Pests: Application and Resistance Management. Springer, Dordrecht, The Netherlands, pp. 1–20.

Hoyt, S.C., Burts, E.C., 1974. Integrated control of fruit pests. Annual Review of Entomology 19, 231–252.

Hull, L.A., Beers, E.H., 1985. Ecological selectivity: modifying chemical control practices to preserve natural enemies. In: Hoy, M.A., Herzog, D.C. (Eds.), Biological Control in Agricultural IPM Systems. Academic Press, New York, pp. 103–122.

Jaynes, H.A., Marucci, P.E., 1947. Effect of artificial control practices on the parasites and predators of the codling moth. Journal of Economic Entomology 40, 9–25.

Johnson, M.T., Tabashnik, B.E., 1999. Enhanced biological control through pesticide selectivity. In: Bellows, T.S., Fisher, T.W. (Eds.), Handbook of Biological Control. Academic Press, New York, pp. 297–317.

Karut, K., Naranjo, S.E., 2009. Mortality factors affecting *Bemisia tabaci* populations on cotton the Çukurova plain, Turkey. Journal of Applied Entomology 133, 367–374.

Lacey, L.A., Fransen, J.J., Carruthers, R., 1996. Global distribution of naturally occurring fungi of *Bemisia*, their biologies and use as biological control agents. In: Gerling, D., Mayer, R.T. (Eds.), *Bemisia* 1995: Taxonomy, Biology, Damage, Control and Management. Intercept Ltd., Andover, Hants, UK, pp. 401–433.

Landis, D.A., Wratten, S.D., Gurr, G.M., 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. Annual Review of Entomology 45, 175–201.

Legendre, P., 2001. Model II Regression — User's Guide. Department of Biological Sciences, University of Montreal. Available from: <http://www.bio.umontreal.ca/casgrain/fr/labo/model-ii.html>.

Littell, R.C., Milliken, G.A., Stroup, W.W., Wolfinger, R.D., 1996. SAS System for Mixed Models. SAS Institute Inc., Cary, NC.

Liu, T.X., Stansly, P.A., 1996. Oviposition, development, and survivorship of *Encarsia pergandiella* (Hymenoptera: Aphelinidae) in four instars of *Bemisia argentifolii* (Homoptera: Aleyrodidae). Annals of the Entomological Society of America 89, 96–102.

Lopez-Avila, A., 1986. Natural enemies. In: Cock, M.J.W. (Ed.), *Bemisia tabaci* — A Literature Survey on the Cotton Whitefly with an Annotated Bibliography. CAB International Institute of Biological Control, Ascot, UK, pp. 27–35.

Musser, F.R., Nyrop, J.P., Shelton, A.M., 2006. Integrating biological and chemical controls in decision making: European corn borer (Lepidoptera: Crambidae) control in sweet corn as an example. Journal of Economic Entomology 99, 1538–1549.

Naranjo, S.E., 2001. Conservation and evaluation of natural enemies in IPM systems for *Bemisia tabaci*. Crop Protection 20, 835–852.

Naranjo, S.E., 2005. Long-term assessment of the effects of transgenic Bt cotton on the abundance of nontarget arthropod natural enemies. Environmental Entomology 34, 1193–1210.

Naranjo, S.E., 2007. Survival and movement of *Bemisia tabaci* (Homoptera: Aleyrodidae) crawlers on cotton. Southwestern Entomologist 32, 17–23.

Naranjo, S.E., Ellsworth, P.C., 2005. Mortality dynamics and population regulation in *Bemisia tabaci*. Entomologia Experimentalis et Applicata 116, 93–108.

Naranjo, S.E., Ellsworth, P.C., 2009. 50 years of the integrated control concept: moving the model and implementation forward in Arizona. Pest Management Science 65

Naranjo, S.E., Ellsworth, P.C., Chu, C.C., Henneberry, T.J., Riley, D.G., Watson, T.F., Nichols, R.L., 1998. Action thresholds for the management of *Bemisia tabaci* (Homoptera: Aleyrodidae) in cotton. Journal of Economic Entomology 91, 1415–1426.

Naranjo, S.E., Ellsworth, P.C., Hagler, J.R., 2004. Conservation of natural enemies in cotton: role of insect growth regulators for management of *Bemisia tabaci*. Biological Control 30, 52–72.

Naranjo, S.E., Flint, H.M., 1994. Spatial distribution of preimaginal *Bemisia tabaci* (Homoptera, Aleyrodidae) in cotton and development of fixed-precision sequential sampling plans. Environmental Entomology 23, 254–266.

Naranjo, S.E., Flint, H.M., 1995. Spatial distribution of adult *Bemisia tabaci* (Homoptera: Aleyrodidae) in cotton and development and validation of fixed-precision sampling plans for estimating population density. Environmental Entomology 24, 261–270.

Naranjo, S.E., Hagler, J.R., Ellsworth, P.C., 2003. Improved conservation of natural enemies with selective management systems for *Bemisia tabaci* (Homoptera: Aleyrodidae) in cotton. Biocontrol Science and Technology 13, 571–587.

Newsom, L.D., Smith, R.F., Whitcomb, W.H., 1976. Selective pesticides and selective use of pesticides. In: Huffaker, C., Messenger, P. (Eds.), Theory and Practice of Biological Control. Academic Press, New York, pp. 565–591.

Podoler, H., Rogers, D., 1975. A new method for the identification of key factors from life-table data. Journal of Animal Ecology 44, 85–114.

Price, J.F., Taborsky, D., 1992. Movement of immature *Bemisia tabaci* (Homoptera, Aleyrodidae) on poinsettia leaves. Florida Entomologist 75, 151–153.

Rabb, R.L., Stinner, R.E., Van den Bosch, R., 1976. Conservation and augmentation of natural enemies. In: Huffaker, C., Messenger, P. (Eds.), Theory and Practice of Biological Control. Academic Press, New York, pp. 233–254.

Royama, T., 1981. Evaluation of mortality factors in insect life table analysis. Ecological Monographs 51, 495–505.

Royama, T., 1996. A fundamental problem in key factor analysis. Ecology 77, 87–93.

Ruberson, J.R., Nemoto, H., Hirose, Y., 1998. Pesticides and conservation of natural enemies in pest management. In: Barbosa, P. (Ed.), Conservation Biological Control. Academic Press, San Diego, CA, pp. 207–220.

Sarvary, M.A., Nyrop, J., Reissig, H., Gifford, K.M., 2007. Potential for conservation biological control of the obliquebanded leafroller (OBLR) *Choristoneura rosaceana* (Harris) in orchard systems managed with reduced-risk insecticides. Biological Control 40, 37–47.

Settle, W.H., Ariawan, H., Astuti, E.T., Cahyana, W., Hakim, A.L., Hindayana, D., Lestari, A.S., Pajarningsih, 1996. Managing tropical rice pest through conservation of generalist natural enemies and alternative prey. Ecology 77, 1975–1988.

Simmons, A.M., 2002. Settling of crawlers of *Bemisia tabaci* (Homoptera: Aleyrodidae) on five vegetable hosts. Annals of the Entomological Society of America 95, 464–468.

Southwood, T.R.E., 1978. Ecological Methods, second ed. Chapman and Hall, London.

Stern, V.M., Smith, R.F., van den Bosch, R., Hagen, K.S., 1959. The integrated control concept. Hilgardia 29, 81–101.

Trumble, J.T., Morse, J.P., 1993. Economics of integrating the predaceous mite *Phytoseilus persimilis* (Acari: Phytoseiidae) with pesticides in strawberries. Journal of Economic Entomology 86, 879–885.

van den Bosch, R., Stern, V.M., 1962. The integration of chemical and biological control of arthropod pests. Annual Review of Entomology 7, 367–386.

van den Bosch, R., Telford, A.D., 1964. Environmental modification and biological control. In: DeBach, P. (Ed.), Biological Control of Insect Pests and Weeds. Reinhold, New York, pp. 459–488.

Varley, G.C., Gradwell, G.R., Hassell, M.P., 1973. Insect Population Ecology: An Analytical Approach. Blackwell Scientific Publications, London.

Waage, J.K., 1989. The population ecology of pest–pesticide–natural enemy interactions. In: Jepson, P.C. (Ed.), Pesticides and Non-target Invertebrates. Intercept Ltd., Andover, Hants, UK, pp. 81–93.

Watson, T.F., Silvertooth, J.C., Tellez, A., Lastra, L., 1992. Seasonal dynamics of sweetpotato whitefly in Arizona. Southwestern Entomologist 17, 149–167.

Zalom, F.G., Hoy, M.A., Wilson, L.T., Barnett, W.W., 1984. Presence-absence sequential sampling for web-spinning mites in almonds. Hilgardia 52, 14–24.

Zalom, F.G., Stimmann, M.W., Arndt, T.S., Walsh, D.B., Pickel, C., Krueger, W.H., 2001. Analysis of permethrin (cis- and trans-isomers) and esfenvalerate on almond twigs and effects of residues on the predator mite *Galendromus occidentalis* (Acari: Phytoseiidae). Environmental Entomology 30, 70–75.