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Conservation of natural enemies in cotton: role of insect growth regulators in management of *Bemisia tabaci*☆

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Abstract

Field studies were conducted from 1997 to 1999 to contrast the effects of two insect growth regulators (IGRs) and conventional insecticides on natural enemy conservation in cotton within the context of alternative management strategies for *Bemisia tabaci* (Gennadius). Compared with an untreated control, insecticide regimes based on the initial use of the IGR buprofezin or pyriproxyfen reduced densities of eight predator taxa out of 20 examined in at least one year, including common species such as *Geocoris punctipes* (Say), *Nabis alternatus* Parshley, *Chrysoperla carnea* s.l., and the empidid fly *Drapetis* nr. *divergens*. Patterns of predator and pest population change relative to IGR application dates suggest that factors other than direct toxic effects, such as reduction in prey availability, were likely involved. In comparison, the use of conventional insecticides reduced populations of nearly all the predatory taxa examined in most years, including those affected by IGRs, with the impact being greater and more immediate in all cases. Predator:prey ratios were significantly increased by the use of IGRs compared with both the untreated control and a conventional insecticide regime in most instances. The application of conventional insecticides for suppression of *Lygus hesperus* Knight, another key pest in the system, in a split-plot design reduced densities of most predator taxa and diminished the selective advantage of the IGRs. Rates of parasitism by aphelinid parasitoids (*Eretmocerus eremicus* Rose and Zolnerowich and *Encarsia* spp.) were generally low and did not vary consistently due to *B. tabaci* or *L. hesperus* insecticide regimes over the three years. Our 3-year study demonstrates the more selective action of buprofezin and pyriproxyfen in an effective integrated control system for *B. tabaci*. The use of these IGRs could further facilitate biologically based management in cotton production systems.
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1. Introduction

The potential of biological control to contribute to pest suppression is limited in many agricultural systems by the use of insecticides with broad toxicity to both the pest and their natural enemies (Croft, 1990). The integrated control concept formalized by Stern et al. (1959) recognizes the important contribution of both chemical and biological control to pest management in agricultural systems. The fundamental components of this concept involve the application of insecticides on the basis of economic thresholds and the use of selective materials, rates, and/or selective application methods that minimize impacts on natural enemy populations (Newsom et al., 1976; Stern et al., 1959).

Bemisia tabaci (Gennadius) Biotype B (= *B. argentifolii* Bellows and Perring) is a cosmopolitan pest of field and horticultural crops (Oliveira et al., 2001). Since the early 1990s, *B. tabaci* has been a key pest of cotton and vegetable crops in the southern US. In Arizona and southern California, large populations of *B. tabaci* develop during summer months in cotton leading to the extensive use of insecticides for whitefly suppression (Ellsworth and Jones, 2001; Ellsworth and Martinez-Carrillo, 2001).

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Although insecticides remain the primary tactic for managing *B. tabaci* in cotton and other affected crops (Palumbo et al., 2001), considerable research has focused on the development of alternative control tactics, including the use of biological control (Gerling and Mayer, 1996; Naranjo and Ellsworth, 2001). Recent reviews have cataloged 114 species of predatory arthropods, nearly 50 species of parasitoids, and 11 species of naturally occurring fungi known to be associated with *B. tabaci* worldwide (Faria and Wraight, 2001; Gerling et al., 2001). In Arizona alone, over 20 species of arthropod predators prey on *B. tabaci* on cotton in the field (Hagler and Naranjo, 1994a,b, unpublished; Hagler, 2002). Several native species of *Eretmocerus* and *Encarsia* parasitize *B. tabaci* in Arizona and southern California (Gerling and Naranjo, 1998; Hoelmer, 1996; Naranjo et al., 2003), and many exotic aphelinid parasitoids have been introduced into the southwestern US over the past decade (Hoelmer and Kirk, 1999; Kirk and Lacey, 1996; Kirk et al., 2001). Life table studies in unsprayed cotton suggest that natural enemies, especially predators, can exert high levels of mortality on immature stages of *B. tabaci* (Naranjo, 2001; Naranjo and Ellsworth, unpublished). The effect of these natural enemies on populations of *B. tabaci* is not completely understood; however, several studies have documented resurgence of *B. tabaci* in cotton with use of broad-spectrum insecticides (Abdelrahman and Munir, 1989; Devine et al., 1998).

Management strategies for *B. tabaci* on cotton in the western US are based on pest monitoring and use of action thresholds to determine the need for insecticides (Ellsworth et al., 1995, 1996b; Naranjo et al., 1998). This approach helped growers maintain profitability in the face of severe pest outbreaks in the early 1990s (Ellsworth and Jones, 2001; Ellsworth and Martinez-Carrillo, 2001). However, the broad-spectrum materials in use severely disrupted natural enemy populations (Naranjo et al., 2002), and over-reliance on these materials led to reduced susceptibility to pyrethroids in *B. tabaci* populations (Dennehy and Williams, 1997; Palumbo et al., 2001). As a result, a US-EPA Section 18 emergency exemption was granted in 1996 for two insect growth regulators (IGRs), buprofezin and pyriproxyfen. Both of these insecticides have been successfully used in Israel for suppression of *B. tabaci* in cotton and greenhouse production for many years (Ishaaya and Horowitz, 1992; Ishaaya et al., 1988) and both materials have low vertebrate toxicity and other qualities that make them relatively safe for the environment (Dhadialla et al., 1998; Pener, 2002).

Extant research on these IGRs indicate that their selectivity varies among arthropod natural enemies. The chitin inhibitor buprofezin has a relatively narrow spectrum of activity against homopterous insects, while pyriproxyfen, a juvenile hormone analog, has a broader spectrum of activity (Dhadialla et al., 1998; Ishaaya et al., 1988). Laboratory bioassay studies have found both compounds to be either benign (Balasubramani and Regupathy, 1994; Castane et al., 1996; Delbeke et al., 1997; Hoddle et al., 2001; Jones et al., 1995; Liu and Stansly, 1997; Peleg, 1988) or toxic (Chen and Liu, 2002; Declercq et al., 1995; Gerling and Sinai, 1994; Hattingh and Tate, 1995; Hoddle et al., 2001; Jones et al., 1998; Liu and Chen, 2000; Magagula and Samways, 2000; Mendel et al., 1994; Smith et al., 1999) to various predators and parasitoids. Few studies have examined the selectivity of these materials in the field (e.g., Naranjo et al., 2003).

Controlled field studies were conducted from 1997 to 1999 to contrast and demonstrate alternative management strategies for *B. tabaci* in Arizona. Based on pest monitoring and action thresholds, a rotation of conventional insecticides was compared with the IGRs buprofezin and pyriproxyfen. The overall project had multiple goals, including evaluation of the efficacy and economics of alternative management regimes (i.e., IGRs) for suppression of *B. tabaci*, refining action thresholds for re-application of the IGRs, evaluation of potential insecticide resistance, and measuring the effects of these alternative management regimes on natural enemy conservation. In this paper we compare the abundance of arthropod predators and aphelinid parasitoids among three different management strategies.

2. Materials and methods

2.1. Study site and experimental design

All studies were conducted at the University of Arizona, Maricopa Agricultural Center, Maricopa, AZ. 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.

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 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 control regimes are denoted by the initial materials used in each regime, and all applications were made on the basis of regular insect sampling and action thresholds (Table 1). In the buprofezin-first regime, the IGR buprofezin was applied at a threshold of

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)	
13 August	pyriproxyfen (60 g/ha)			
20 August		buprofezin (392 g/ha)	fenpropathrin (224 g/ha) + acephate (561 g/ha)	
4 September	endosulfan (841 g/ha) + amitraz (280 g/ha)	endosulfan (841 g/ha) + amitraz (280 g/ha)	endosulfan (841 g/ha) + amitraz (280 g/ha)	
12 September	oxamyl (561 g/ha) + profenophos (841 g/ha)	oxamyl (561 g/ha) + profenophos (841 g/ha)	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 /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.

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., 1996b). This was followed 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. This label also permitted only a single use of each IGR per season. 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, 1996a). A final regime was left untreated for *B. tabaci* to serve as the control. In the 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*. In 1997 only, the split-plot design was incomplete in that the "conventional" control regime was not split for *L. hesperus* control. Instead the entire whole plot was sprayed for *L. hesperus* as needed. All applications were made by tractor-mounted ground sprayers. Seasonal usage of insecticides is summarized in Table 1.

2.2. Pest sampling

Densities of *B. tabaci* eggs, nymphs, and adults were estimated each week from early July through late September or early October each year. Nymphal and egg densities were estimated by counting individuals (at 10× on a dissecting microscope) on a 3.88 cm^2 disk taken from the fifth mainstem leaf below the terminal (Naranjo and Flint, 1994). Nymphs were categorized as either small (first or second instar) or large (third or

fourth instar) for the purpose of threshold implementation (see above). Adult density was estimated by counting individuals, in situ, on the underside of leaves from the fifth mainstem node below the terminal (Naranjo and Flint, 1995). Ten sample units were randomly collected per plot for immature and adult stages on each sample date. Decisions to apply insecticides were based on the average densities in four replicate plots. Densities of *L. hesperus* were monitored weekly from early July onward using a standard 38-cm diameter sweep net. A total of 50 sweeps were taken per plot and decisions to spray were made on the basis of counts from all treated split-plots.

2.3. Natural enemy sampling

Arthropod predators were sampled each week with a standard 38-cm diameter sweep net from early June through mid to late September each year. Two sets of 25 sweeps (50 total) were collected in each plot using a random starting point. Samples were frozen and later sorted in the laboratory with the aid of a dissecting microscope. Densities of 20 taxa of arthropod predators were estimated. Immature and adult stages of most taxa were pooled for analyses. *L. hesperus*, *Pseudatomoscelis seriatus* (Reuter), *Spanogonicus albofasciatus* (Reuter), and *Rhinacloa forticornis* Reuter were included because these species may exhibit omnivorous feeding habits (Agnew et al., 1982; Butler, 1965; Hagler and Naranjo, 1994a, unpublished). Only larval stages of the green lacewing were counted, and following Tauber et al. (2000) we used the designation of *Chrysoperla carnea* sensu lato for this species. Voucher specimens reside in the Department of Entomology, University of Arizona, Tucson, research collection.

Predator:prey ratios were calculated as the quotient of all predators combined (per 50 sweeps) to the number of *B. tabaci* eggs, nymphs, adults, or all life stages per leaf combined. Egg and nymphal densities per leaf were estimated from regression models relating disk to whole leaf counts (Naranjo and Flint, 1994). Predator:prey ratios calculated for contrasts involving *L. hesperus* control excluded *L. hesperus* and *P. seriatus*, because these insects were the primary targets of control.

Densities of immature aphelinid parasitoids (*Eretmocerus* spp. and *Encarsia* spp.) were estimated by taking leaf samples (20–30 per plot) from the seventh mainstem node below the terminal. Samples were collected weekly from early July through mid to late September each year. In the laboratory all larval and pupal parasitoids of each genus (when possible) and all unparasitized fourth instar whitefly nymphs on the entire leaf were counted. The presence of visible larvae or meconia within the host mummy was used to discriminate *Encarsia* spp. from *Eretmocerus* spp. after parasitoids reached later larval or pupal stages. Displacement of the host's mycetomes was used to determine the presence of young parasitoid larvae, but in these cases the genus of the parasitoid could not be discerned. An index of parasitism was calculated based on the proportion of fourth instar nymphs parasitized by both genera combined. A subsample of leaves from each plot was held to determine the species composition from emerged adults.

2.4. Statistical analyses

Mixed-model, repeated measures analysis of variance (Littell et al., 1996) was used to test for treatment differences over the season each year. 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. The first order heterogeneous autoregressive option (ARH1 in SAS Proc Mixed) was used to estimate the repeated measures covariance structure, as it consistently maximized Akaike's Information and Schwarz' Bayesian Criteria (Littell et al., 1996). Pre-planned orthogonal contrasts were used to compare both IGR regimes with the control and the conventional regime, to compare the conventional regime and the control, and to contrast the two IGR regimes. Treatment effects on proportional parasitism were analyzed with the SAS macro, GLIMMIX (Littell et al., 1996), which performs mixed-model ANOVA using a binomial error structure. Because the split-plot (*L. hesperus* control regime) design was incomplete in 1997, two sets of analyses were performed. A split-plot ANOVA was conducted after excluding the conventional regime, which was not split for *L. hesperus* control. A randomized complete block ANOVA was then conducted for all four whitefly control regimes that were treated with insecticides for control of *L. hesperus*. Arthropod counts and predator:prey ratios were transformed by $(x+0.5)^{0.5}$ or $\ln(x+1)$ throughout as necessary to achieve normality and homoscedasticity before analyses; untransformed means are presented. Analyses were limited to sample dates following the first application of insecticides for *B. tabaci*.

A meta-analysis was performed to summarize treatment effects over all three years. Indices were calculated as the mean of the product $p_i s_i$ over all years, where p is the proportional reduction in density of each predator taxa, parasitism, or predator–prey ratio in a given insecticide regime relative to the untreated control in year i, and s is a dummy variable indicating the statistical significance ($s = 1$) or non-significance ($s = 0$) of the reduction based on ANOVA. Additionally, mean proportional reductions (relative to the control) in predator densities, parasitism, and predator:prey ratios were calculated.

To further examine seasonal treatment effects on arthropod predator populations, a time-dependent, multivariate analysis called principal response curves (PRC)

(van den Brink and Ter Braak, 1998, 1999) was conducted. PRC is based on an ordination method known as partial redundancy analysis, a type of principal component analysis in which information is extracted only from the variance explained by treatment effects. PRC provide a simple means of visualizing and testing the overall response of a biological community to environmental stress by determining treatment effects relative to an untreated control. The program CANOCO 4 (Ter Braak and Smilauer, 1998) was used to perform the partial redundancy analyses, construct the PRC, and test for treatment differences in community composition using a distribution-free F type test based on sample permutation. In CANOCO, the analyses can be structured to account for blocking and split-plot effects and to allow statistical inference for individual dates or the entire season. Treatment contrasts similar to those for ANOVA above were performed. For analyses of *L. hesperus* control effects, we excluded *L. hesperus* and *P. seriatus*. Arthropod count data were transformed by $\ln(x+1)$ prior to analysis.

3. Results

In all three years, the first insecticide applications were made for control of *L. hesperus* in mid to late July (Table 1). A single application was made for this pest in 1997, but three applications were necessary in 1998 and 1999. The first insecticide applications for *B. tabaci* varied from late July to early August. In 1997, both IGR regimes required sprays of buprofezin and pyriproxyfen plus the application of two conventional insecticides late in the season. The conventional regime was sprayed five times over the course of the season. In 1998 and 1999 only a single application of either buprofezin or pyriproxyfen was needed in either IGR regime. In the conventional regime, one and three applications were necessary in 1998 and 1999, respectively.

3.1. Pest populations

Detailed analyses of treatment effects on densities of *B. tabaci*, yields, and overall economics are presented elsewhere (Ellsworth and Naranjo, 1999; Ellsworth et al., 1998; Ellsworth and Naranjo, unpublished data); only general results will be briefly discussed here. Population densities of *B. tabaci* varied over the years of the study, but were generally highest in 1997 and lowest in 1998. Densities of all *B. tabaci* stages were reduced in all whitefly control regimes compared with the untreated control in all years. Densities of eggs and adults were consistently lowest in the conventional regime and generally significantly higher ($P < 0.05$) in the two IGR regimes. All whitefly control regimes were equally effective in reducing densities of nymphs in all years. The effect of *L. hesperus* control on densities of *B. tabaci* were minor; however, significant seasonal reductions ($P < 0.05$) were measured in eggs (1999) and nymphs (1998 and 1999), with variable impact on adults in 1997 and 1998.

3.2. Predator populations and predator:prey ratios

Many predator taxa occurred at relatively low densities over the three years of the study, especially beetles, most spiders, and several heteropterans. The most abundant spider was the crab spider, *Misumenops celer* (Hentz), while *Orius tristicolor* (White) and *Geocoris punctipes* (Say) were consistently the most common predaceous heteropterans. The plant pest and facultative predator *L. hesperus* consistently occurred at high densities, and *P. seriatus* was relatively abundant in 1997 and 1998. Larval *C. carnea* s.l. were relatively abundant, and adults of the empidid fly, *Drapetis* nr. *divergens*, were the most abundant predator species observed over the entire study.

There were no significant ($P > 0.05$) interactions between *B. tabaci* and *L. hesperus* control regimes for any taxa; thus, only main effects are presented. Sufficient numbers of immature *G. punctipes*, *O. tristicolor*, *L. hesperus*, and *P. seriatus* were available for separate analyses. However, in all cases results for immature and adult stages were similar, and so only results for adults and immatures combined are reported.

3.2.1. 1997

Based on split-plot analyses of predator densities excluding the conventional insecticide regime, seasonal average densities of five out of 19 taxa were significantly reduced ($P < 0.05$) in the IGR regimes compared with the control, including *G. punctipes*, *Nabis alternatus* Parshley, *L. hesperus*, *C. carnea* s.l., and *D.* nr. *divergens* (Table 2). No significant differences ($P > 0.05$) were detected for any taxa between the two IGR regimes. The use of insecticides for *L. hesperus* control significantly reduced ($P < 0.05$) the densities of seven predator taxa including most of those negatively affected by the IGRs (Table 2). The seasonal average density of the target, *L. hesperus*, was reduced by over 38%. Predator:prey ratios were significantly higher ($P < 0.05$) in the IGR regimes compared with the control. Predator:prey ratios did not differ between the two IGR regimes, but the addition of insecticides for *L. hesperus* suppression significantly reduced ($P < 0.05$) these ratios. Predator:prey ratios varied over the season, but were consistently higher in plots not receiving additional insecticides for *L. hesperus* control (Fig. 1B).

Results from analyses based only on split-plots receiving *L. hesperus* control in 1997 were similar to those for the IGR regimes above. The exceptions were that seasonal average densities of *D.* nr. *divergens* in the IGR

Table 2
Seasonal mean densities (per 50 sweeps) of arthropod predators, predator to prey ratios, and parasitism under various control regimes for *B. tabaci* and *L. hesperus*, Maricopa, AZ, 1997

	B. tabaci control regime			Orthogonal contrasts[a]-*F* values		*L. hesperus* control		
	Buprofezin 1st	Pyriproxyfen 1st	Control	IGR vs Control	Bup vs Pyr	No	Yes	F^a
Dictyna reticulata	0.05 ± 0.03	0.13 ± 0.11	0.16 ± 0.04	1.94 (1)	1.26 (1)	0.15 ± 0.06	0.07 ± 0.05	2.58 (1)
Misumenops celer	0.77 ± 0.19	1.05 ± 0.16	0.98 ± 0.08	0.70 (1)	0.89 (0)	1.35 ± 0.12	0.51 ± 0.15	21.9** (4)
Jumping spiders	0.14 ± 0.06	0.23 ± 0.10	0.13 ± 0.05	0.86 (0)	1.42 (0)	0.20 ± 0.06	0.14 ± 0.04	0.49 (0)
Other spiders	0.39 ± 0.13	0.44 ± 0.13	0.44 ± 0.11	0.26 (0)	0.02 (0)	0.51 ± 0.16	0.33 ± 0.09	1.52 (2)
Collops vittatus	0.23 ± 0.07	0.28 ± 0.14	0.25 ± 0.06	0.00 (0)	0.03 (0)	0.31 ± 0.11	0.20 ± 0.04	0.87 (0)
Hippodamia convergens	0.13 ± 0.04	0.09 ± 0.02	0.09 ± 0.02	0.09 (1)	0.28 (0)	0.10 ± 0.04	0.10 ± 0.03	0.01 (1)
Other coccinellids	0.06 ± 0.06	0.09 ± 0.02	0.06 ± 0.01	0.15 (0)	0.46 (0)	0.10 ± 0.03	0.04 ± 0.03	2.76 (0)
Anthicidae	0.16 ± 0.06	0.14 ± 0.05	0.17 ± 0.07	0.08 (1)	0.03 (1)	0.18 ± 0.03	0.14 ± 0.07	0.51 (0)
Geocoris punctipes	0.94 ± 0.09	0.84 ± 0.21	2.16 ± 0.34	25.2** (5)	0.20 (0)	1.92 ± 0.17	0.71 ± 0.10	30.3** (5)
Geocoris pallens	0.08 ± 0.03	0.13 ± 0.04	0.17 ± 0.03	1.45 (1)	0.59 (1)	0.20 ± 0.03	0.05 ± 0.02	6.00* (3)
Orius tristicolor	5.94 ± 0.88	6.42 ± 0.41	6.77 ± 0.53	0.32 (1)	0.03 (0)	6.57 ± 0.49	6.18 ± 0.60	0.01 (1)
Nabis alternatus	0.06 ± 0.03	0.08 ± 0.05	0.30 ± 0.09	13.4** (2)	0.07 (0)	0.13 ± 0.04	0.17 ± 0.05	0.70 (0)
Zelus renardii	0.38 ± 0.11	0.42 ± 0.16	0.59 ± 0.12	2.14 (2)	0.05 (0)	0.55 ± 0.08	0.38 ± 0.02	2.39 (1)
Sinea spp.	0.09 ± 0.04	0.09 ± 0.07	0.20 ± 0.07	3.21 (1)	0.02 (0)	0.15 ± 0.03	0.11 ± 0.02	0.30 (1)
Lygus hesperus	10.8 ± 0.74	9.66 ± 1.07	15.6 ± 1.13	33.3** (5)	2.11 (0)	14.9 ± 0.37	9.17 ± 0.36	18.7** (4)
Pseudatomoscelis seriatus	1.05 ± 0.30	1.41 ± 0.44	1.61 ± 0.35	1.32 (1)	0.44 (0)	1.91 ± 0.39	0.80 ± 0.23	15.2** (3)
Spanogonicus albofasciatus	0.19 ± 0.00	0.17 ± 0.05	0.27 ± 0.05	1.33 (1)	0.05 (0)	0.24 ± 0.05	0.18 ± 0.05	0.67 (1)
Chrysoperla carnea s.l.	3.50 ± 0.29	3.33 ± 0.30	5.89 ± 0.48	6.59* (2)	0.04 (0)	4.89 ± 0.34	3.59 ± 0.22	12.6* (3)
Drapetis nr. *divergens*	25.3 ± 2.55	23.4 ± 2.07	35.2 ± 3.28	9.46* (3)	0.13 (0)	33.5 ± 2.22	22.3 ± 1.35	7.45* (4)
Pred:Prey Ratio (Eggs)[b]	0.35 ± 0.04	0.37 ± 0.02	0.22 ± 0.04	9.56* (4)	0.05 (0)	0.26 ± 0.02	0.19 ± 0.02	16.2** (3)
Pred:Prey Ratio (Nymphs)[b]	0.82 ± 0.06	0.70 ± 0.03	0.45 ± 0.05	32.3** (5)	0.02 (0)	0.59 ± 0.03	0.41 ± 0.03	21.5** (4)
Pred:Prey Ratio (Adults)[b]	10.9 ± 1.34	11.6 ± 1.13	5.82 ± 0.54	26.7** (4)	0.52 (0)	9.18 ± 0.93	5.37 ± 0.69	20.5** (4)
Pred:Prey Ratio (All)[b]	0.22 ± 0.01	0.21 ± 0.02	0.13 ± 0.02	13.1** (4)	0.08 (0)	0.17 ± 0.01	0.11 ± 0.01	19.0** (4)
Prop. Parasitism[c]	0.06 ± 0.01	0.13 ± 0.03	0.09 ± 0.02	1.45 (1)	13.2** (4)	0.06 ± 0.01	0.10 ± 0.02	6.69* (2)

Values are mean seasonal densities ± SE over eight post-treatment sample dates in four replicate plots ($n = 4$). Analyses do not include the conventional regime for *B. tabaci* control because the split-plot was incomplete for this regime (i.e., entire whole plot treated for *L. hesperus*). IGR=buprofezin + pyriproxyfen; Bup=buprofezin 1st regime; Pyr=pyriproxyfen 1st regime.

[a] Repeated-measures ANOVA using Proc Mixed (Littell et al., 1996); d.f. estimated by Satterthwaite's correction; $^*P < 0.05$; $^{**}P < 0.01$; values in parentheses indicate the number of sample dates (out of 8 total) on which the *F*-value was significant ($P < 0.05$).

[b] Quotient of all arthropod predators per 50 sweeps to *B. tabaci* eggs, nymphs, adults or all life stages combined per leaf. For *L. hesperus* control contrasts, the ratio does not include densities of *L. hesperus* or *P. seriatus*.

[c] Proportion of 4th instar *B. tabaci* nymphs parasitized per leaf.

regimes did not differ ($P > 0.05$) from the control (Table 3). The application of conventional insecticides had a predictable, negative effect on predator populations, significantly reducing ($P < 0.05$) densities of 12 of the 19 taxa compared with the control. Seasonal average densities of seven taxa were significantly higher ($P < 0.05$) in the IGR regimes compared with the conventional regime, including most of the spiders, and several beetles and heteropterans. Densities of *Hippodamia convergens* Guérin-Méneville were significantly greater ($P < 0.05$) in the buprofezin regime compared with the pyriproxyfen regime (Table 3). The opposite was true for the "other spiders" group.

Densities of predators varied significantly ($P < 0.05$) over time, but there were relatively few significant time interactions with either *B. tabaci* or *L. hesperus* control regimes (four and five taxa out of 20, respectively). In these cases, interactions arose primarily from small changes in density differences among insecticide regimes on a few sampling dates. Usually, these changes occurred at relatively low predator densities.

Seasonal average predator:prey ratios based on *B. tabaci* nymphs and adults were significantly higher ($P < 0.05$) for the IGR regimes compared with the control and the nymph-based ratio was significantly higher for the IGR compared with the conventional regime (Table 3). There were no differences in any ratio between the conventional regime and the control, or between the two IGR regimes ($P > 0.05$). Predator:prey ratios varied significantly ($P < 0.05$) over time, but were generally highest in the IGR regimes and lowest in the conventional regime over most sample dates (Fig. 1A). There was a significant time by *B. tabaci* control regime interaction ($P < 0.05$) in predator:prey ratios; this was largely a function of small changes in differences between the two IGR regimes over sampling dates.

The time-dependent effect of control regimes on the predator community was further examined using

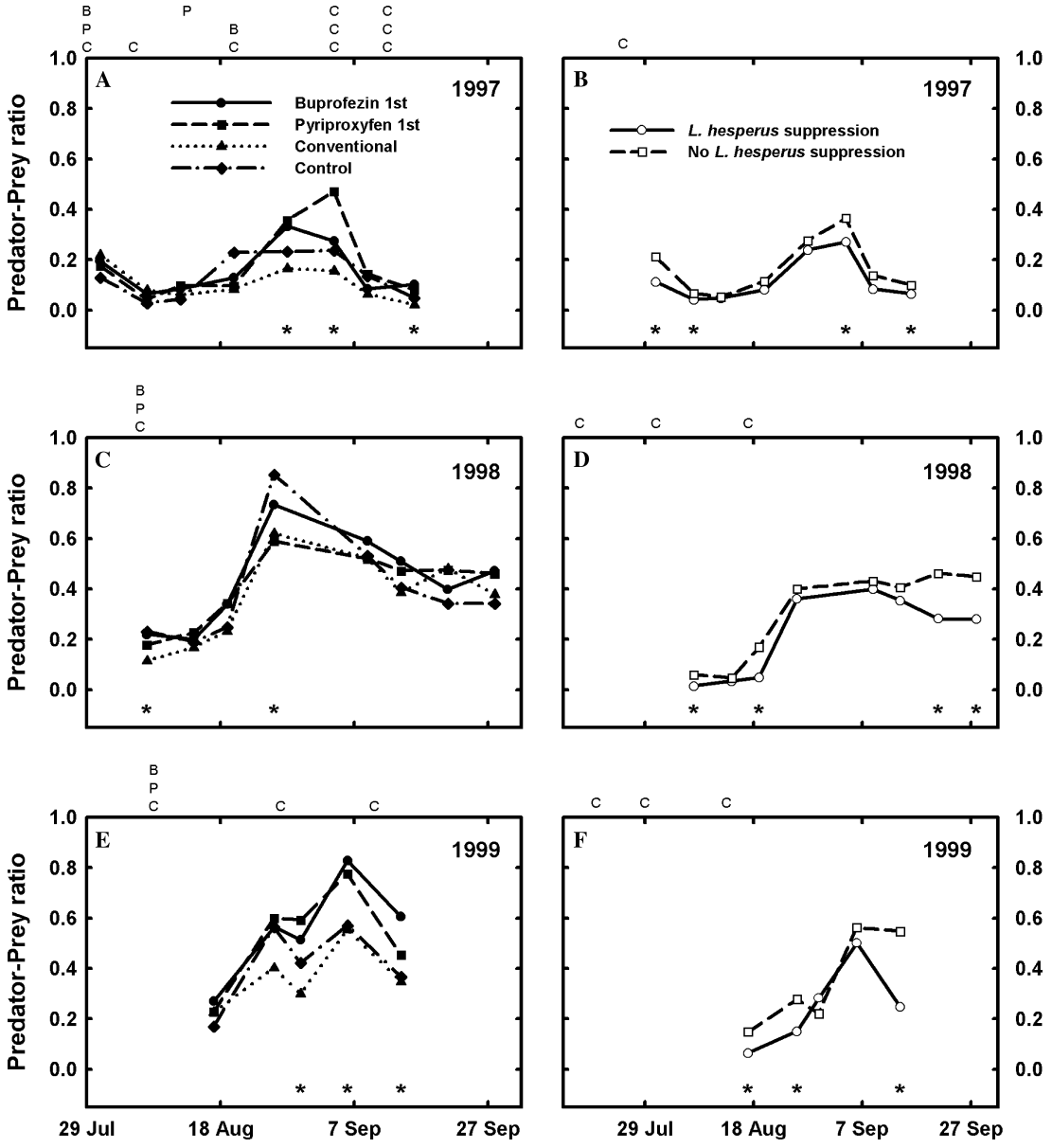

Fig. 1. The main effects of *B. tabaci* (A, C, E) and *L. hesperus* (B, D, F) control regimes on total predator to prey ratios during the growing season, 1997–1999, Maricopa, AZ. Only post-application dates for whitefly insecticides are shown. The predator–prey ratio is estimated as the quotient of all arthropod predators (per 50 sweeps) to all *B. tabaci* life stages per leaf. Asterisks along the bottom of each graph denote dates on which significant ($P < 0.05$) treatment differences were observed; letters along the top of each graph denote the timing of applications of buprofezin (B), pyriproxyfen (P) or conventional (C) insecticides. Results in A are based solely on data from split-plots receiving *L. hesperus* control, because the split-plot design was incomplete in 1997.

principal response curves (PRC). Results of analyses based on the split-plots receiving *L. hesperus* control are presented in Fig. 2A. The PRC based on the first axis of the redundancy analysis were highly significant ($P < 0.01$) and explained 51% of the variation due to control regime. The second axis explained an additional 12% of the variance, but was not significant ($P = 0.85$). Negative canonical coefficients indicate that populations of predators were generally lower in the insecticide regimes compared with the untreated control. Contrasts based on permutation tests over all sample dates combined indicated IGR and conventional regimes significantly reduced ($P < 0.05$) the density of the predator community compared with the untreated control. However, as with the univariate analyses, predator densities were significantly ($P < 0.05$) lower in the conventional compared with the IGR regimes. There was no difference ($P > 0.05$) between the two IGR regimes. Date by date contrasts indicate that neither IGR regime differed from the control until the last two sampling dates following the two applications of conventional insecticides (Fig. 2A). In contrast, the repeated

Table 3
Seasonal mean densities (per 50 sweeps) of arthropod predators, predator to prey ratios, and parasitism under different control regimes for *B. tabaci*, Maricopa, AZ, 1997

	B. tabaci control regime				Orthogonal contrasts[a]—*F* values			
	Buprofezin 1st	Pyriproxyfen 1st	Conventional	Control	IGR vs Control	IGR vs Conven	Conven vs Control	Bup vs Pyr
Dictyna reticulata	0.01 ± 0.00	0.16 ± 0.12	0.01 ± 0.00	0.06 ± 0.04	0.01 (0)	1.24 (0)	0.82 (0)	3.71 (2)
Misumenops celer	0.41 ± 0.09	0.53 ± 0.16	0.09 ± 0.06	0.59 ± 0.22	0.97 (1)	6.42* (3)	9.27** (4)	0.38 (1)
Jumping spiders	0.16 ± 0.06	0.19 ± 0.11	0.01 ± 0.00	0.06 ± 0.04	1.99 (1)	5.07* (3)	0.53 (0)	0.06 (0)
Other spiders	0.16 ± 0.09	0.47 ± 0.19	0.03 ± 0.03	0.38 ± 0.05	0.60 (0)	5.18* (2)	6.98** (4)	4.26* (1)
Collops vittatus	0.19 ± 0.06	0.19 ± 0.04	0.06 ± 0.04	0.22 ± 0.03	0.14 (0)	12.3** (4)	11.0** (4)	0.01 (0)
Hippodamia convergens	0.16 ± 0.03	0.03 ± 0.03	0.03 ± 0.03	0.13 ± 0.05	0.42 (0)	1.68 (0)	2.84 (0)	5.05* (1)
Other coccinellids	0.06 ± 0.06	0.03 ± 0.03	0.03 ± 0.03	0.03 ± 0.03	0.10 (0)	0.10 (0)	0.00 (0)	0.29 (0)
Anthicidae	0.16 ± 0.08	0.16 ± 0.09	0.06 ± 0.06	0.09 ± 0.06	1.14 (0)	5.67* (3)	0.08 (0)	0.01 (0)
Geocoris punctipes	0.31 ± 0.06	0.56 ± 0.26	0.22 ± 0.08	1.25 ± 0.21	14.7** (3)	1.09 (0)	17.8** (4)	0.58 (0)
Geocoris pallens	0.01 ± 0.00	0.06 ± 0.04	0.09 ± 0.03	0.09 ± 0.03	2.03 (1)	2.03 (1)	0.01 (1)	1.52 (0)
Orius tristicolor	5.91 ± 1.21	6.03 ± 0.69	2.63 ± 0.58	6.59 ± 1.02	0.06 (1)	16.2** (5)	13.7** (4)	0.01 (0)
Nabis alternatus	0.09 ± 0.03	0.09 ± 0.06	0.06 ± 0.06	0.31 ± 0.11	6.40* (2)	0.31 (0)	7.15* (3)	0.01 (0)
Zelus renardii	0.25 ± 0.11	0.31 ± 0.23	0.06 ± 0.06	0.56 ± 0.13	2.71 (0)	1.40 (1)	6.00* (3)	0.09 (0)
Sinea spp.	0.03 ± 0.03	0.13 ± 0.09	0.01 ± 0.00	0.19 ± 0.06	2.33 (0)	1.21 (1)	5.18* (2)	1.02 (0)
Lygus hesperus	8.09 ± 0.89	6.78 ± 1.16	4.13 ± 0.55	12.6 ± 0.92	26.6** (2)	15.1** (4)	61.3** (6)	0.86 (0)
Pseudatomoscelis seriatus	0.47 ± 0.34	0.75 ± 0.42	0.22 ± 0.08	1.19 ± 0.36	2.49 (1)	1.49 (2)	5.88* (2)	0.59 (0)
Spanogonicus albofasciatus	0.19 ± 0.04	0.19 ± 0.11	0.06 ± 0.04	0.16 ± 0.06	0.20 (0)	2.16 (2)	0.79 (0)	0.01 (0)
Chrysoperla carnea s.l.	3.03 ± 0.48	2.41 ± 0.24	3.28 ± 0.59	5.34 ± 0.79	7.81* (3)	0.01 (2)	5.37* (3)	0.44 (0)
Drapetis nr. *divergens*	19.6 ± 3.27	22.1 ± 2.23	15.8 ± 3.78	25.1 ± 3.50	1.45 (0)	1.51 (1)	4.89* (1)	0.43 (0)
Pred:Prey Ratio (Eggs)[b]	0.29 ± 0.06	0.29 ± 0.04	0.22 ± 0.04	0.18 ± 0.03	2.43 (2)	0.17 (1)	0.98 (1)	0.06 (0)
Pred:Prey Ratio (Nymphs)[b]	0.60 ± 0.10	0.61 ± 0.03	0.36 ± 0.05	0.34 ± 0.02	11.2** (4)	9.59** (3)	0.04 (1)	0.30 (0)
Pred:Prey Ratio (Adults)[b]	7.75 ± 2.02	8.25 ± 0.71	7.26 ± 0.80	4.79 ± 0.41	5.03* (3)	0.41 (1)	1.89 (2)	0.40 (0)
Pred:Prey Ratio (All)[b]	0.16 ± 0.03	0.18 ± 0.02	0.13 ± 0.02	0.11 ± 0.02	3.45 (2)	0.82 (0)	0.67 (2)	0.01 (0)
Prop. Parasitism[c]	0.05 ± 0.01	0.11 ± 0.04	0.04 ± 0.01	0.06 ± 0.02	1.70 (1)	1.41 (1)	0.01 (0)	5.46* (2)

Values are mean seasonal densities ± SE over eight post-treatment sample dates in four replicate plots ($n = 4$). Analyses based only on split plots receiving *L. hesperus* control. IGR=buprofezin + pyriproxyfen; Bup=buprofezin 1st regime; Pyr=pyriproxyfen 1st regime; Conven=conventional whitefly control regime.

[a] Repeated-measures ANOVA using Proc Mixed (Littell et al., 1996); d.f. estimated by Satterthwaite's correction; $^{*}P < 0.05$; $^{**}P < 0.01$; values in parentheses indicate the number of sample dates (out of 8 total) on which the *F*-value was significant ($P < 0.05$).

[b] Quotient of all arthropod predators per 50 sweeps to *B. tabaci* eggs, nymphs, adults or all life stages combined per leaf.

[c] Proportion of 4th instar *B. tabaci* nymphs parasitized per leaf.

application of insecticides in the conventional regime depressed predator densities on multiple dates throughout the growing season and these reductions followed the pattern of application. A single application of oxamyl for *L. hesperus* in late July resulted in a large initial reduction in predator populations (Fig. 2B). Populations rebounded in early to mid-August but were significantly lower compared with the untreated control in late August and early September. The PRC based on the first axis of the redundancy analysis was highly significant ($P < 0.01$) and explained 71% of the variation. The second axis explained an additional 9%, but was not significant ($P = 0.75$).

The species weights denote the strength of the response for each individual taxa (Fig. 2). The higher the value the more the response of a given taxa resembles the PRC. Negative weights indicate an opposite pattern and values between −0.5 and 0.5 indicate a weak response or a response unrelated to the PRC (van den Brink and Ter Braak, 1999). Species weights suggest that the PRC for the both the *B. tabaci* and *L. hesperus* control regimes are most representative of *L. hesperus*, *O. tristicolor*, *G. punctipes*, *C. carnea* s.l., *P. seriatus*, *D.* nr. *divergens*, *M. celer*, *Zelus renardii* Kolenati, and the "other spider" group.

3.2.2. 1998

Seasonal average densities of only *D.* nr. *divergens* and *S. albofasciatus* were significantly reduced ($P < 0.05$) in the IGR regimes compared with the control, while densities of the "other spider" group increased significantly in the IGR regimes (Table 4). In contrast, densities of 11 taxa were significantly reduced ($P < 0.05$) in the conventional regime compared with the control. For 10 predator taxa, densities were significantly higher ($P < 0.05$) in the IGR compared with the conventional regime (Table 4). There were no significant differences ($P > 0.05$) between the two IGR regimes for any predator taxa. Insecticides for control of *L. hesperus* significantly reduced ($P < 0.05$) seasonal average densities of 16 predator taxa (Table 4). The seasonal average density of the target, *L. hesperus*, was reduced by over 52%.

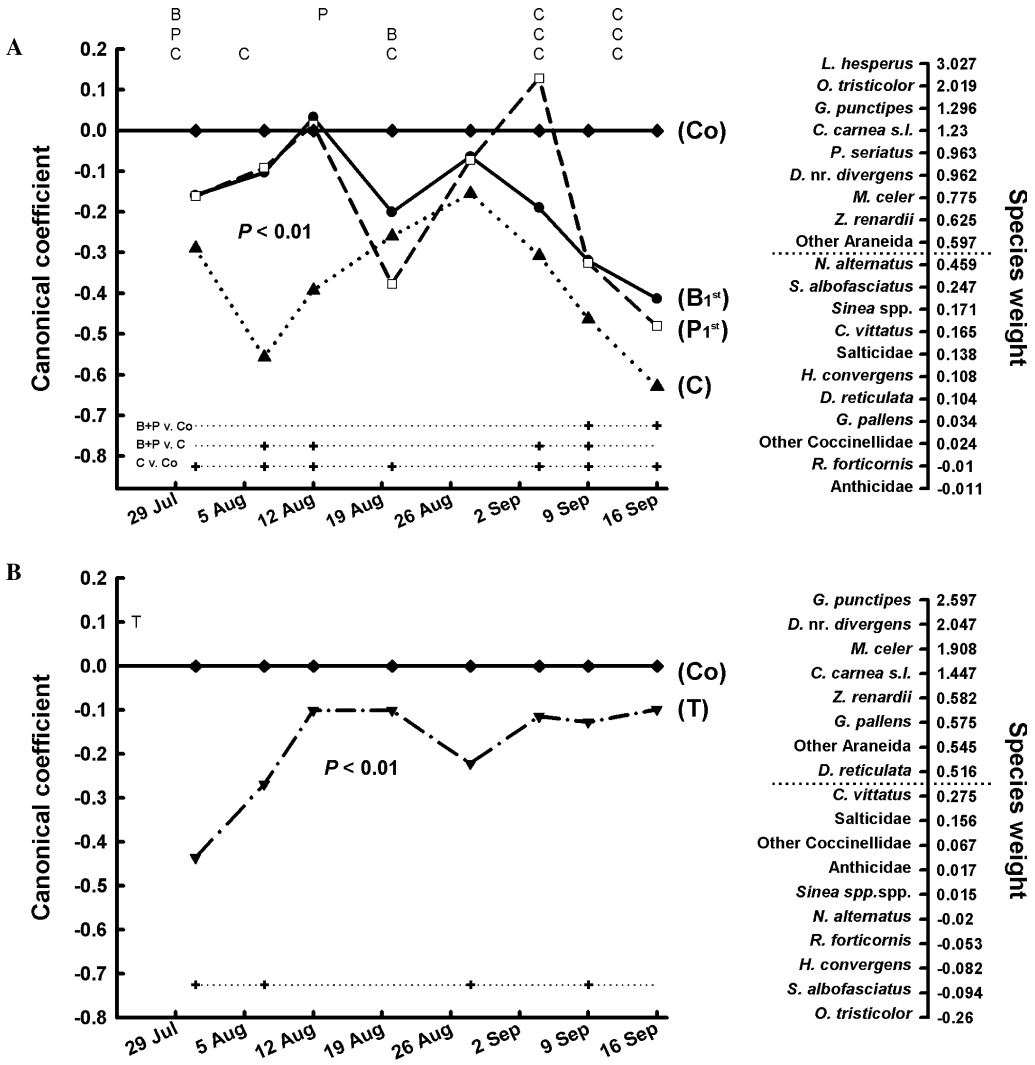

Fig. 2. Principal response curves (PRC) showing the main effects of (A) whitefly control (only post-application dates for whitefly insecticides are shown), and (B) *L. hesperus* control (only post-application dates for *L. hesperus* insecticides are shown) on the predatory arthropod community during the growing season, 1997, Maricopa, AZ. The PRC show the effect of each treatment regime relative to the untreated control (Co) which is represented by the $y = 0$ line. The greater the species weight the more the response for that species resembles the PRC. Negative weights indicate an opposite pattern, and weights between −0.5 and 0.5 indicate a weak response or a response unrelated to the PRC. The *P*-value denotes the significance of the PRC analysis over all dates based on an *F*-type permutation test. The plus symbols at the base of each graph denote the significance ($P < 0.05$) of the indicated contrast on each date determined by *F*-type permutation test; letters along the top of each graph denote the timing of applications of buprofezin (B), pyriproxyfen (P), or conventional insecticides for whitefly (C) or *L. hesperus* (T). There were no significant differences between the two IGRs on any date and so contrasts are not shown. Results in A are based solely on data from split-plots receiving *L. hesperus* control, because the split-plot design was incomplete in 1997.

Most predator densities varied significantly ($P < 0.05$) over time and significant time by *B. tabaci* control regime interactions were observed for *D.* nr. *divergens* and *L. hesperus*. These interactions arose from small differences in insecticide effects on two or three sampling dates. Significant time by *L. hesperus* control interactions were detected for seven taxa and this was primarily due to small changes in insecticide effects on one or two sampling dates.

Predator:prey ratios based on *B. tabaci* adults were significantly higher ($P < 0.05$) in the IGR and conventional regimes compared with the control and ratios based on nymphs were significantly higher ($P < 0.05$) in the IGR compared with the conventional regime (Table 4). Predator:prey ratios based on all *B. tabaci* stages combined varied significantly ($P < 0.05$) over time (Fig. 1C). Significant treatment differences were only observed during the first four sample dates following insecticide application; however, ratios were numerically lowest in the conventional regime over a large portion of the season. Predator:prey ratios based on eggs, nymphs and all stages combined were significantly reduced ($P < 0.05$) with the addition of insecticides for *L. hesperus* control (Table 4, Fig. 1D). There

Table 4
Seasonal mean densities (per 50 sweeps) of arthropod predators, predator to prey ratios, and parasitism under various control regimes for *B. tabaci* and *L. hesperus*, Maricopa, AZ, 1998

	B. tabaci control regime				Orthogonal contrasts[a]—*F* values				*L. hesperus* control		
	Buprofezin 1st	Pyriproxyfen 1st	Conven	Control	IGR vs Control	IGR vs Conven	Conven vs Control	Bup vs Pyr	No	Yes	*F*[a]
Dictyna reticulata	0.42 ± 0.06	0.38 ± 0.05	0.33 ± 0.10	0.50 ± 0.11	0.03 (0)	0.89 (0)	0.92 (0)	0.28 (0)	0.56 ± 0.02	0.25 ± 0.07	7.33* (3)
Misumenops celer	8.79 ± 0.76	8.59 ± 0.22	6.58 ± 0.32	7.67 ± 0.32	2.10 (1)	15.5* (4)	4.63* (3)	0.02 (0)	10.5 ± 0.54	5.34 ± 0.24	116** (7)
Jumping spiders	1.70 ± 0.23	1.79 ± 0.14	1.50 ± 0.26	1.72 ± 0.14	0.02 (1)	1.20 (0)	0.66 (2)	0.02 (0)	1.98 ± 0.15	1.37 ± 0.08	10.4** (3)
Other spiders	1.95 ± 0.29	1.77 ± 0.34	1.70 ± 0.17	1.20 ± 0.27	5.35* (1)	1.36 (0)	0.99 (0)	0.66 (0)	2.02 ± 0.28	1.29 ± 0.34	11.3** (3)
Collops vittatus	0.39 ± 0.08	0.26 ± 0.04	0.16 ± 0.05	0.48 ± 0.06	2.54 (1)	6.22* (2)	13.1** (3)	2.40 (1)	0.36 ± 0.06	0.29 ± 0.05	1.51 (1)
Hippodamia convergens	0.19 ± 0.03	0.23 ± 0.09	0.09 ± 0.06	0.20 ± 0.09	0.35 (1)	3.80 (0)	1.37 (2)	0.45 (0)	0.27 ± 0.04	0.09 ± 0.03	9.8* (3)
Other coccinellids	0.05 ± 0.04	0.11 ± 0.05	0.11 ± 0.09	0.13 ± 0.05	0.27 (0)	0.05 (0)	0.37 (0)	0.37 (1)	0.19 ± 0.10	0.01 ± 0.01	4.58* (2)
Anthicidae	0.41 ± 0.23	0.66 ± 0.29	0.11 ± 0.03	0.47 ± 0.20	0.09 (1)	5.40* (3)	4.70* (1)	1.41 (1)	0.41 ± 0.04	0.41 ± 0.02	0.40 (0)
Geocoris punctipes	1.34 ± 0.32	1.32 ± 0.22	0.83 ± 0.18	1.39 ± 0.13	0.05 (0)	7.60** (2)	4.77* (2)	0.00 (0)	1.91 ± 0.24	0.53 ± 0.07	59.2** (6)
Geocoris pallens	0.41 ± 0.04	0.48 ± 0.10	0.17 ± 0.05	0.48 ± 0.03	0.01 (1)	9.38** (3)	6.65* (3)	0.43 (1)	0.48 ± 0.06	0.29 ± 0.03	4.47* (3)
Orius tristicolor	6.13 ± 0.39	4.87 ± 0.21	5.09 ± 0.47	7.09 ± 0.49	3.46 (1)	1.10 (0)	6.37* (2)	2.45 (0)	6.25 ± 0.49	5.35 ± 0.49	6.25* (4)
Nabis alternatus	0.16 ± 0.02	0.13 ± 0.03	0.06 ± 0.01	0.14 ± 0.05	0.01 (0)	5.26* (2)	2.27 (1)	0.13 (0)	0.16 ± 0.02	0.08 ± 0.01	5.48* (2)
Zelus renardii	3.18 ± 0.20	2.94 ± 0.37	2.73 ± 0.22	3.25 ± 0.35	0.84 (1)	1.38 (1)	3.27 (1)	0.24 (0)	3.92 ± 0.15	2.13 ± 0.17	87.3** (6)
Sinea spp.	0.23 ± 0.07	0.23 ± 0.05	0.28 ± 0.13	0.14 ± 0.07	1.42 (0)	0.02 (0)	0.85 (0)	0.00 (0)	0.27 ± 0.07	0.18 ± 0.07	0.96 (0)
Lygus hesperus	24.7 ± 1.09	24.5 ± 1.38	20.1 ± 1.17	24.0 ± 1.47	0.00 (0)	19.9** (4)	15.2** (5)	0.18 (0)	31.6 ± 1.52	15.0 ± 0.78	128** (6)
Pseudatomoscelis seriatus	1.41 ± 0.08	1.28 ± 0.20	0.73 ± 0.26	1.56 ± 0.12	0.10 (0)	9.21** (3)	8.41** (3)	0.59 (0)	1.78 ± 0.05	0.71 ± 0.12	32.4** (6)
Spanogonicus albofasciatus	0.16 ± 0.04	0.11 ± 0.02	0.09 ± 0.02	0.36 ± 0.12	7.12* (1)	0.62 (0)	8.94** (2)	0.58 (0)	0.18 ± 0.03	0.18 ± 0.03	0.00 (0)
Rhinacloa forticornis	0.66 ± 0.12	0.55 ± 0.12	0.55 ± 0.19	0.78 ± 0.22	1.07 (0)	0.39 (0)	0.42 (0)	0.39 (0)	0.91 ± 0.18	0.36 ± 0.13	17.2** (4)
Chrysoperla carnea s.l.	1.78 ± 0.12	1.56 ± 0.11	1.46 ± 0.17	1.88 ± 0.27	0.01 (0)	5.33* (2)	4.08* (1)	0.06 (0)	2.16 ± 0.09	1.17 ± 0.10	27.1** (5)
Drapetis nr. *divergens*	8.00 ± 1.45	6.21 ± 1.64	6.27 ± 0.76	13.2 ± 5.64	5.58* (1)	5.91* (3)	14.9** (4)	4.86 (2)	11.3 ± 3.26	5.57 ± 1.47	28.1** (6)
Pred:Prey Ratio (Eggs)[b]	0.84 ± 0.07	0.77 ± 0.07	0.93 ± 0.04	0.76 ± 0.07	1.66 (1)	0.69 (2)	3.38 (2)	0.91 (1)	0.61 ± 0.04	0.45 ± 0.06	26.7** (4)
Pred:Prey Ratio (Nymphs)[b]	1.07 ± 0.07	1.06 ± 0.07	0.96 ± 0.03	0.98 ± 0.08	2.39 (1)	7.22* (4)	1.09 (3)	0.05 (0)	0.70 ± 0.06	0.49 ± 0.05	46.9** (5)
Pred:Prey Ratio (Adults)[b]	19.9 ± 1.24	22.6 ± 1.24	23.4 ± 0.63	15.0 ± 2.85	15.7** (3)	1.02 (4)	18.3** (4)	1.82 (1)	12.9 ± 0.44	11.7 ± 1.42	1.09 (2)
Pred:Prey Ratio (All)[b]	0.43 ± 0.03	0.41 ± 0.03	0.44 ± 0.02	0.39 ± 0.03	1.81 (0)	0.24 (2)	0.55 (2)	0.46 (0)	0.30 ± 0.02	0.22 ± 0.03	35.1** (4)
Prop. parasitism[c]	0.13 ± 0.02	0.12 ± 0.02	0.14 ± 0.02	0.14 ± 0.02	0.02 (0)	0.11 (0)	0.16 (1)	2.13 (2)	0.16 ± 0.02	0.11 ± 0.01	6.41* (2)

Values are mean seasonal densities ± SE over eight post-treatment sample dates in four replicate plots ($n = 4$). IGR=buprofezin + pyriproxyfen; Bup=buprofezin 1st regime; Pyr=pyriproxyfen 1st regime; Conven=conventional whitefly control regime.

[a] Repeated-measures ANOVA using Proc Mixed (Littell et al., 1996); d.f. estimated by Satterthwaite's correction; $^{*}P < 0.05$; $^{**}P < 0.01$; values in parentheses indicate the number of sample dates (out of 8 total) on which the *F*-value was significant ($P < 0.05$).

[b] Quotient of all arthropod predators per 50 sweeps to *B. tabaci* eggs, nymphs, adults or all life stages combined per leaf. For *L. hesperus* control contrasts, the ratio does not include densities of *L. hesperus* or *P. seriatus*.

[c] Proportion of 4th instar *B. tabaci* nymphs parasitized per leaf.

were significant ($P < 0.05$) time by *B. tabaci* control regime interactions. This was largely due to inconsistent treatment effects over time, especially among the IGR regimes and the untreated control (Fig. 1C). The effect of *L. hesperus* control on predator:prey ratios was consistent and no interaction with time was detected ($P > 0.05$).

PRC for *B. tabaci* control regimes based on the first axis of the redundancy analysis were significant ($P < 0.01$) and explained 38% of the variation due to treatment regime (Fig. 3A). The second axis explained an additional 13% of the variance, but was not significant ($P = 0.41$). Contrasts based on permutation tests for all sample dates combined indicated that the conventional, but not the IGR regimes, significantly reduced ($P < 0.05$) the overall density of predators compared with the untreated control. Predator densities also were significantly lower ($P < 0.05$) in conventional compared with the IGR regimes. There was no difference ($P > 0.05$) between the two IGR regimes. Date by date contrasts indicated that the IGR regimes differed from the control on a singe date in early September well after insecticide applications. In contrast, a single application of conventional insecticides in early August initially reduced predator densities for two weeks

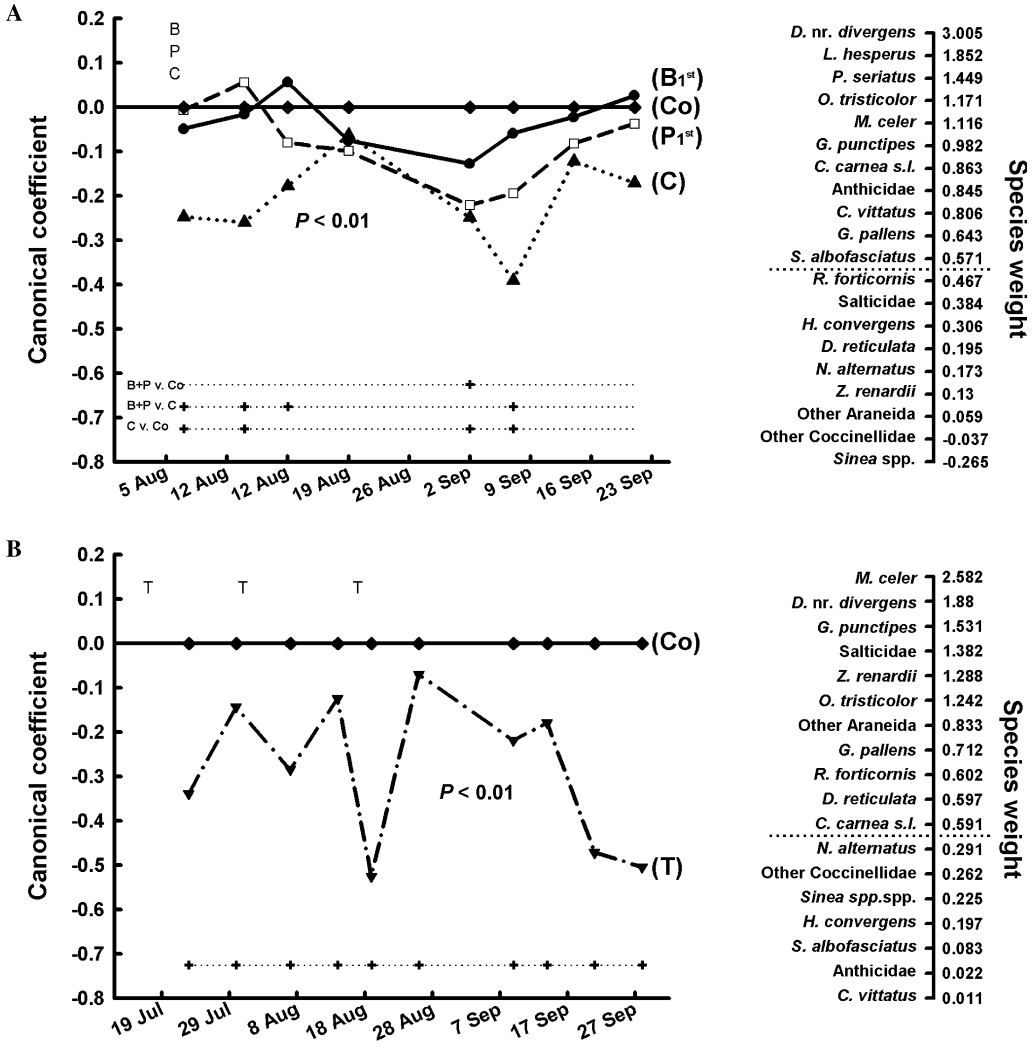

Fig. 3. Principal response curves (PRC) showing the main effects of (A) whitefly control (only post-application dates for whitefly insecticides are shown), and (B) *L. hesperus* control (only post-application dates for *L. hesperus* insecticides are shown) on the predatory arthropod community during the growing season, 1998, Maricopa, AZ. The PRC show the effect of each treatment regime relative to the untreated control (Co) which is represented by the $y = 0$ line. The greater the species weight the more the response for that species resembles the PRC. Negative weights indicate an opposite pattern and weights between −0.5 and 0.5 indicate a weak response or a response unrelated to the PRC. The *P*-value denotes the significance of the PRC analysis over all dates based on an *F*-type permutation test. The plus symbols at the base of each graph denote the significance ($P < 0.05$) of the indicated contrast on each date determined by *F*-type permutation test; letters along the top of each graph denote the timing of applications of buprofezin (B), pyriproxyfen (P), or conventional insecticides for whitefly (C) or *L. hesperus* (T). There were no significant differences between the two IGRs on any date and so contrasts are not shown.

following the spray and led to significant reductions ($P < 0.05$) from early to mid-September. Species weights indicate that the PRC were representative of 11 out of 20 taxa with the highest weights associated with *D*. nr. *divergens*, *L. hesperus*, *P. seriatus*, *O. tristicolor*, *M. celer*, and *G. punctipes* (Fig. 3A). Repeated applications of conventional insecticides for control of *L. hesperus* had a strong negative effect on predator populations throughout the entire season with marked reductions following each of the three applications in mid to late July and mid-August (Fig. 3B). The PRC based on the first axis of the redundancy analysis was highly significant ($P < 0.01$) and explained 68% of the variation due to insecticide application for *L. hesperus*. The second axis explained an additional 13%, but was not significant ($P = 0.18$). Species weights indicate that the PRC were representative of 11 out of 18 taxa with the highest weights associated with *M. celer*, *D*. nr. *divergens*, *G. punctipes*, salticid spiders, *Z. renardii* and *O. tristicolor* (Fig. 3B).

3.2.3. 1999

Seasonal average densities of four out of 19 predator taxa were significantly reduced ($P < 0.05$) in the IGR regimes compared with the control including *M. celer*, other coccinellids, *C. carnea* s.l. and *D*. nr. *divergens* (Table 5). In contrast, densities of nine predator taxa were significantly reduced ($P < 0.05$) in the conventional regime compared with the control (Table 5). Seasonal average densities of 10 predator taxa were significantly higher ($P < 0.05$) in the IGR compared with the conventional regime (Table 5). There were no significant ($P > 0.05$) differences between the two IGR regimes for any predator taxa. *L. hesperus* control significantly ($P < 0.05$) reduced the densities of 12 predator taxa (Table 5). The seasonal average density of the target, *L. hesperus*, was reduced by about 52%.

Predator densities varied significantly ($P < 0.05$) over the growing season, and significant time by *B. tabaci* control regime interactions were observed for six taxa. In most cases these interactions resulted from inconsistent treatment effects that occurred at relatively low densities. Significant time by *L. hesperus* control interactions were detected for *O. tristicolor* and *D*. nr. *divergens*. For the former, the interaction arose due to an increase in density in the sprayed regime on a single date in early September. For *D*. nr. *divergens* reductions in density in the sprayed plots were magnified on the last two sampling dates.

All predator:prey ratios were significantly higher ($P < 0.05$) in the IGR compared with the control, and ratios based on nymphs and all stages combined were significantly higher ($P < 0.05$) in IGR compared with the conventional regime (Table 5). The nymphal-based ratio was higher in the control compared with the conventional regime; all ratios were similar between the IGR regimes. Predator:prey ratios varied over time, and significant treatment differences ($P < 0.05$) were observed on the final three sampling dates (Fig. 1E.). Ratios were generally higher in IGR and lowest in conventional regimes over most of the growing season. Predator:prey ratios based on eggs, nymphs, and on all stages combined were significantly reduced ($P < 0.05$) with the addition of insecticides for *L. hesperus* control, and this pattern was generally consistent over the season (Table 5, Fig. 1F). There were significant ($P < 0.05$) time by *B. tabaci* control regime interactions resulting primarily from the variable effects between the two IGR regimes and the inconsistent pattern in the control relative to the conventional regime (Fig. 1E). There was a significant ($P < 0.05$) time by *L. hesperus* control interaction that was due mainly to the response in the untreated control on the third sampling date (Fig. 1F).

PRC for the *B. tabaci* control regime based on the first axis of the redundancy analysis were highly significant ($P < 0.01$) and explained 51% of the variation due to treatment regime. The second axis explained an additional 12% of the variance, but was not significant ($P = 0.27$). Contrasts based on permutation tests for all sample dates combined indicated that both the IGR and conventional regimes significantly reduced ($P < 0.05$) the overall density of the predator community compared with the untreated control (Fig. 4A). However, again, reductions in predator density were significantly greater ($P < 0.05$) in the conventional compared with the IGR regimes. There was no difference ($P > 0.05$) between the two IGR regimes. Date by date contrasts showed that the IGR regimes differed from the control on two sample dates towards the latter part of the growing season many weeks following insecticide applications (Fig. 4A). In the conventional regime significant reductions in predator densities were associated with each of the three insecticide applications. Species weights indicate that the PRC were most representative of *M. celer*, *G. punctipes*, *L. hesperus*, *O. tristicolor*, *D*. nr. *divergens*, *C. carnea* s.l., other coccinellids and spiders, and *Collops vittatus* Say (Fig. 4A). Repeated applications of insecticides for control of *L. hesperus* negatively affected predator populations throughout the entire season with marked reductions following each application (Fig. 4B). PRC based on the first axis of the redundancy analysis was highly significant ($P < 0.01$) and explained 76% of the variation. The second axis explained an additional 14%, but again, was not significant ($P = 0.15$). Species weights indicate that the PRC was most representative of *D*. nr. *divergens*, *O. tristicolor*, *G. punctipes*, *M. celer*, *C. carnea* s.l., *H. convergens*, and several spider taxa (Fig. 4B).

3.3. Parasitoid populations and parasitism

Eretmocerus eremicus Rose and Zolnerowich and *Encarsia* spp. (mainly *E. meritoria* Gahan) were found

Table 5
Seasonal mean densities (per 50 sweeps) of arthropod predators, predator to prey ratios, and parasitism under various control regimes for *B. tabaci* and *L. hesperus*, Maricopa, AZ, 1999

	B. tabaci control regime				Orthogonal contrasts[a]—*F* values				*L. hesperus* control		
	Buprofezin 1st	Pyriproxyfen 1st	Conven	Control	IGR vs Control	IGR vs Conven	Conven vs Control	Bup vs Pyr	No	Yes	*F*[a]
Dictyna reticulata	0.27 ± 0.15	0.30 ± 0.17	0.28 ± 0.18	0.33 ± 0.19	0.62 (1)	0.99 (1)	1.17 (1)	0.03 (0)	0.32 ± 0.10	0.06 ± 0.05	11.0** (2)
Misumenops celer	2.00 ± 0.39	1.70 ± 0.23	0.72 ± 0.09	2.97 ± 0.18	16.6* (2)	26.8** (2)	64.2** (3)	1.49 (1)	2.35 ± 0.33	1.59 ± 0.06	5.43* (2)
Jumping spiders	0.47 ± 0.13	0.42 ± 0.09	0.17 ± 0.05	0.30 ± 0.07	1.19 (1)	5.88* (2)	0.58 (0)	0.26 (0)	0.42 ± 0.11	0.28 ± 0.05	1.66 (0)
Other spiders	1.08 ± 0.22	1.72 ± 0.34	0.95 ± 0.22	1.38 ± 0.26	0.38 (0)	6.98* (2)	3.07 (1)	2.61 (0)	1.57 ± 0.26	0.81 ± 0.13	11.5** (2)
Collops vittatus	0.70 ± 0.20	0.48 ± 0.18	0.40 ± 0.04	0.68 ± 0.05	0.30 (1)	0.86 (0)	1.63 (1)	1.01 (0)	0.76 ± 0.09	0.39 ± 0.06	6.21* (2)
Other coccinellids	0.45 ± 0.14	0.22 ± 0.05	0.13 ± 0.08	0.85 ± 0.28	6.92* (1)	5.43* (1)	13.2** (3)	1.73 (0)	0.69 ± 0.18	0.24 ± 0.04	6.42* (2)
Anthicidae	0.40 ± 0.04	0.23 ± 0.11	0.35 ± 0.10	0.47 ± 0.14	1.12 (0)	0.07 (0)	0.47 (0)	1.37 (1)	0.41 ± 0.07	0.35 ± 0.06	0.07 (0)
Geocoris punctipes	1.40 ± 0.15	1.58 ± 0.37	0.30 ± 0.09	1.85 ± 0.13	1.01 (0)	19.3** (4)	21.3** (4)	0.52 (0)	1.89 ± 0.18	0.59 ± 0.17	35.2** (4)
Geocoris pallens	0.08 ± 0.05	0.20 ± 0.08	0.03 ± 0.03	0.05 ± 0.03	1.31 (0)	2.39 (0)	0.12 (0)	1.67 (1)	0.16 ± 0.05	0.04 ± 0.02	2.72 (4)
Orius tristicolor	8.53 ± 1.52	7.45 ± 0.36	5.72 ± 0.67	9.25 ± 1.36	0.88 (1)	7.47* (2)	9.89** (3)	1.35 (1)	10.4 ± 1.25	6.27 ± 0.47	21.9** (4)
Nabis alternatus	0.28 ± 0.08	0.23 ± 0.05	0.10 ± 0.04	0.25 ± 0.06	0.21 (0)	6.27* (2)	6.93** (2)	0.19 (0)	0.30 ± 0.04	0.13 ± 0.03	6.89* (2)
Zelus renardii	0.15 ± 0.06	0.05 ± 0.03	0.03 ± 0.03	0.15 ± 0.12	0.46 (0)	1.46 (0)	2.68 (1)	1.95 (1)	0.12 ± 0.04	0.07 ± 0.03	0.32 (0)
Sinea spp.	0.05 ± 0.03	0.01 ± 0.01	0.01 ± 0.01	0.05 ± 0.03	0.80 (0)	0.80 (0)	2.40 (1)	2.40 (0)	0.03 ± 0.02	0.03 ± 0.01	0.00 (0)
Lygus hesperus	23.3 ± 2.32	22.9 ± 0.63	14.9 ± 1.36	25.8 ± 0.98	2.20 (1)	26.3** (4)	32.8** (4)	0.08 (0)	31.6 ± 2.35	15.2 ± 0.72	95.0** (4)
Pseudatomoscelis seriatus	0.47 ± 0.21	0.30 ± 0.15	0.15 ± 0.12	0.55 ± 0.18	0.12 (0)	1.99 (0)	6.30* (2)	0.65 (0)	0.53 ± 0.19	0.17 ± 0.06	3.27 (1)
Spanogonicus albofasciatus	0.03 ± 0.03	0.10 ± 0.04	0.08 ± 0.05	0.13 ± 0.05	1.49 (0)	0.06 (0)	0.72 (0)	1.61 (0)	0.15 ± 0.02	0.08 ± 0.03	0.09 (0)
Rhinacloa forticornis	0.22 ± 0.13	0.15 ± 0.06	0.15 ± 0.09	0.33 ± 0.13	1.44 (0)	0.24 (0)	2.15 (0)	0.23 (0)	0.30 ± 0.03	0.09 ± 0.03	8.86** (2)
Chrysoperla carnea s.l.	3.88 ± 0.60	2.95 ± 0.13	2.38 ± 0.30	4.65 ± 0.70	7.03* (2)	6.90* (2)	16.5** (3)	2.90 (1)	3.79 ± 0.35	3.05 ± 0.23	5.79* (2)
Drapetis nr. *divergens*	31.3 ± 2.99	26.4 ± 3.75	22.6 ± 3.74	38.4 ± 4.98	6.00* (1)	9.91** (3)	23.5** (4)	1.52 (0)	37.6 ± 4.08	18.4 ± 1.96	63.1** (3)
Pred:Prey Ratio (Eggs)[b]	1.12 ± 0.17	0.98 ± 0.14	0.77 ± 0.10	0.69 ± 0.19	10.1** (2)	3.11 (2)	1.49 (0)	2.00 (0)	0.68 ± 0.04	0.54 ± 0.05	5.19* (3)
Pred:Prey Ratio (Nymphs)[b]	1.29 ± 0.10	1.39 ± 0.11	0.89 ± 0.05	1.01 ± 0.09	6.04* (2)	19.6** (3)	4.43* (1)	0.02 (1)	0.91 ± 0.08	0.63 ± 0.05	18.0** (3)
Pred:Prey Ratio (Adults)[b]	19.7 ± 3.32	24.1 ± 5.29	20.3 ± 3.72	15.9 ± 3.77	5.89* (2)	0.05 (0)	2.94 (1)	0.25 (1)	14.4 ± 3.56	12.5 ± 1.88	3.44 (1)
Pred:Prey Ratio (All)[b]	0.55 ± 0.07	0.51 ± 0.05	0.35 ± 0.04	0.40 ± 0.08	7.82* (2)	9.74** (3)	0.07 (0)	0.72 (0)	0.37 ± 0.03	0.25 ± 0.02	6.15* (3)
Prop. Parasitism[c]	0.02 ± 0.01	0.03 ± 0.01	0.04 ± 0.01	0.03 ± 0.01	0.20 (0)	3.46 (1)	1.54 (1)	0.03 (1)	0.04 ± 0.01	0.02 ± 0.01	0.63 (0)

Values are means seasonal densities ± SE over five post-treatment sample dates in four replicate plots ($n = 4$). IGR = buprofezin + pyriproxyfen; Bup = buprofezin 1st regime; Pyr = pyriproxyfen 1st regime; Conven = conventional whitefly control regime.

[a] Repeated-measures ANOVA using Proc Mixed (Littell et al., 1996); d.f. estimated by Satterthwaite's correction; $^{*}P < 0.05$; $^{**}P < 0.01$; values in parentheses indicate the number of sample dates (out of 8 total) on which the *F*-value was significant ($P < 0.05$).

[b] Quotient of all arthropod predators per 50 sweeps to *B. tabaci* eggs, nymphs, adults or all life stages combined per leaf. For *L. hesperus* control contrasts, the ratio does not include densities of *L. hesperus* or *P. seriatus*.

[c] Proportion of 4th instar *B. tabaci* nymphs parasitized per leaf.

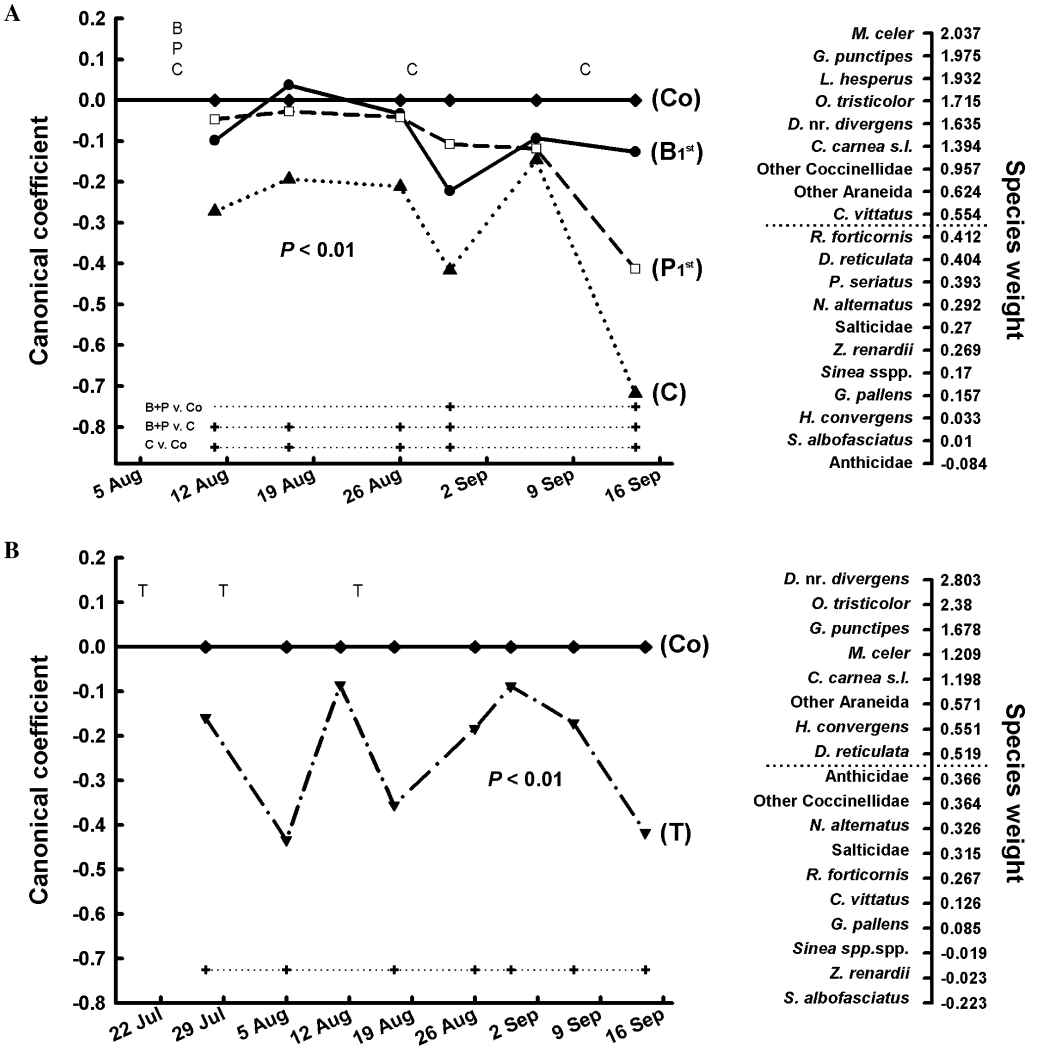

Fig. 4. Principal response curves (PRC) showing the main effects of (A) whitefly control (only post-application dates for whitefly insecticides are shown), and (B) *L. hesperus* control (only post-application dates for *L. hesperus* insecticides are shown) on the predatory arthropod community during the growing season, 1999, Maricopa, AZ. The PRC show the effect of each treatment regime relative to the untreated control (Co) which is represented by the $y = 0$ line. The greater the species weight the more the response for that species resembles the PRC. Negative weights indicate an opposite pattern and weights between −0.5 and 0.5 indicate a weak response or a response unrelated to the PRC. The *P*-value denotes the significance of the PRC analysis over all dates based on an *F*-type permutation test. The plus symbols at the base of each graph denote the significance ($P < 0.05$) of the indicated contrast on each date determined by *F*-type permutation test; letters along the top of each graph denote the timing of applications of buprofezin (B), pyriproxyfen (P), or conventional insecticides for whitefly (C) or *L. hesperus* (T). There were no significant differences between the two IGRs on any date and so contrasts are not shown.

attacking *B. tabaci* at our study site. *Eretmocerus* spp. were dominant, comprising over 85, 59, and 55% of all parasitoids sampled in 1997, 1998, and 1999, respectively. As with predators there were no significant ($P > 0.05$) interactions between *B. tabaci* and *L. hesperus* control regimes in parasitism rates and so only main effects are presented. The proportion of parasitized hosts varied widely in 1997 ranging from <0.05 on several sample dates in all regimes to >0.30 by mid-August in the pyriproxyfen regime (Fig. 5A). Averaged over the season, there were few significant differences among whitefly control regimes with the highest rate of parasitism being observed in the pyriproxyfen regime (Tables 2 and 3). In 1998, rates of parasitism increased steadily over the season in all whitefly control regimes with rates exceeding 0.25 by mid September (Fig. 5C). Seasonal average rates of parasitism did not differ significantly ($P > 0.05$) among whitefly control regimes (Table 4), although rates of parasitism differed significantly, but not consistently, on several sample dates. Rates of parasitism were low in 1999, rarely exceeding 0.10 in any regime and there were no significant differences ($P > 0.05$) among whitefly control regimes (Table 5, Fig. 5E). The rate of parasitism was significantly higher with *L. hesperus* suppression in 1997 (Table 2), but significantly higher without *L. hesperus* control in

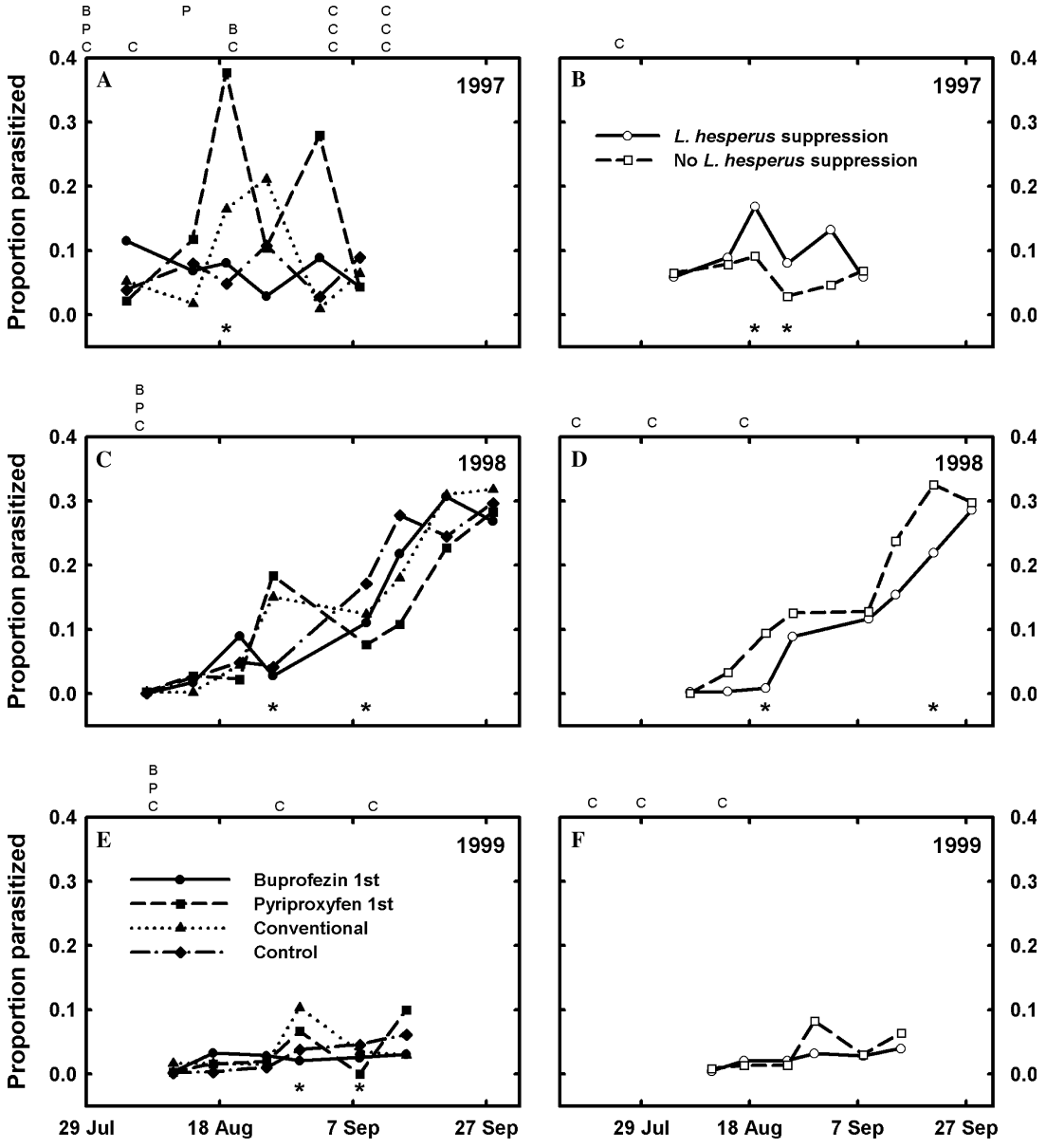

Fig. 5. The main effects of *B. tabaci* (A, C, E) and *L. hesperus* (B, D, F) control regimes on proportional parasitism by aphelinid parasitoids attacking *B. tabaci* during the growing season, 1997–1999, Maricopa, AZ. Only post-application dates for whitefly insecticides are shown. Asterisks along the bottom of each graph denote dates on which significant ($P < 0.05$) treatment differences were observed; letters along the top of each graph denote the timing of applications of buprofezin (B), pyriproxyfen (P) or conventional (C) insecticides. Results in A are based solely on data from split-plots receiving *L. hesperus* control, because the split-plot design was incomplete in 1997.

1998 (Table 4). These patterns resulted largely from relatively small differences in parasitism on several sample dates and the differing intervals between samples and *L. hesperus* spray applications in the two years (Figs. 5B and D). There was no effect ($P > 0.05$) of *L. hesperus* control on rates of parasitism in 1999 (Table 5, Fig. 5F).

Rates of parasitism varied significantly ($P < 0.05$) over time, and there were significant whitefly control regime by date interactions in all years. These interactions were due to the inconsistent effects of the treatment regimes over the course of each season (Fig. 5). There were no significant ($P > 0.05$) interactions between *L. hesperus* control regimes and time.

3.4. Overall impact of insecticides

To summarize results from all three years, indices were calculated based on statistically significant changes in seasonal densities of each predator taxa, rates of parasitism, and predator:prey ratios relative to the untreated control (Table 6). *M. celer*, other coccinellids,

Table 6
Meta-analysis of the effect of *B. tabaci* and *L. hesperus* control on arthropod predators, predator to prey ratios, and parasitism over a three year period, Maricopa, AZ, 1997–1999

	B. tabaci control regime				*L. hesperus* control	
	IGR 1st		Conventional			
Dictyna reticulata	0[a]	(0.74)	0	(0.28)	−0.46	(0.37)
Misumenops celer	−0.13	(0.85)	−0.58	(0.42)	−0.48	(0.52)
Jumping spiders	0	(1.81)	0	(0.54)	−0.10	(0.69)
Other spiders	0.18	(1.13)	−0.31	(0.73)	−0.28	(0.60)
Collops vittatus	0	(0.80)	−0.46	(0.40)	−0.16	(0.65)
Hippodamia convergens	0	(0.59)	0	(0.23)	−0.22	(0.44)
Other coccinellids	−0.20	(0.84)	−0.28	(0.67)	−0.53	(0.27)
Anthicidae	0	(1.20)	−0.26	(0.55)	0	(0.88)
Geocoris punctipes	−0.22	(0.70)	−0.69	(0.31)	−0.68	(0.32)
Geocoris pallens	0	(1.37)	−0.22	(0.65)	−0.38	(0.37)
Orius tristicolor	0	(0.85)	−0.42	(0.58)	−0.18	(0.80)
Nabis alternatus	−0.24	(0.78)	−0.47	(0.34)	−0.36	(0.75)
Zelus renardii	0	(0.70)	−0.30	(0.38)	−0.15	(0.61)
Sinea spp.	0	(0.89)	−0.32	(0.75)	0	(0.80)
Lygus hesperus	−0.14	(0.84)	−0.42	(0.58)	−0.48	(0.52)
Pseudatomoscelis seriatus	0	(0.69)	−0.69	(0.31)	−0.39	(0.38)
Spanogonicus albofasciatus	−0.21	(0.69)	−0.25	(0.41)	0	(0.76)
Rhinacloa forticornis	0	(0.45)	0	(0.39)	−0.43	(0.23)
Chrysoperla carnea s.l.	−0.25	(0.71)	−0.37	(0.63)	−0.31	(0.69)
D. nr. *divergens*	−0.24	(0.71)	−0.44	(0.56)	−0.45	(0.55)
Pred:Prey Ratio (Eggs)	0.17	(1.40)	0	(1.19)	−0.25	(0.75)
Pred:Prey Ratio (Nymphs)	0.37	(1.40)	0.04	(0.97)	−0.30	(0.70)
Pred:Prey Ratio (Adults)	0.49	(1.49)	0.19	(1.40)	−0.14	(0.79)
Pred:Prey Ratio (All)	0.11	(1.32)	0	(1.06)	−0.31	(0.69)
Proportional parasitism	0	(1.02)	0	(1.00)	0.12	(0.95)

[a] Index is calculated as the mean of $p_i s_i$ over all three years, where p is the proportional change in predator density, parasitism, or the predator–prey ratio in a given insecticide regime relative to the control in year i and s is a dummy variable indicating the statistical significance ($s = 1$) or non-significance ($s = 0$) of the reduction based on ANOVA results in year i. Values in parentheses indicate the mean (all years) density, ratio or parasitism rate as a proportion of the control level.

G. punctipes, *N. alternatus*, *L. hesperus*, *S. albofasciatus*, *C. carnea* s.l., and *D.* nr. *divergens* were all significantly reduced by the use of either IGR regime relative to the control in at least one year. For the "other spiders" group, densities were significantly higher under the IGR regimes. These same predators plus eight additional taxa were significantly reduced by the conventional insecticide regime relative to the control. In all instances the negative impact of conventional insecticides was greater than that of the IGRs. Mean predator population densities in insecticide regimes viewed as a proportion of the untreated control (Table 6, values in parentheses) further emphasize the selective nature of the IGRs. Average densities of some taxa (jumping spiders, other spiders, anthicid beetle, *G. pallens*) were higher in the IGR regimes than in the untreated control. Predator:prey ratios based on each *B. tabaci* stage separately and all stages combined increased with the use of IGRs with changes being largest for ratios based on nymphs and adults. Predator:prey ratios based on nymphs or adults increased slightly in the conventional regime compared with the control and were 1.3 to 1.5 times higher in IGR regimes than in the control. With the exception of anthicid beetles, *Sinea* spp. and *S. albofasciatus*, the application of insecticides for control of *L. hesperus* significantly reduced densities of all predator taxa and all predator:prey ratios (Table 6). In many cases these reductions were relatively large. Parasitism increased slightly with *L. hesperus* control, but was unaffected by any whitefly insecticide regime.

4. Discussion

Enhancing the role of biological control within insecticide-dominated management systems will require insecticides and application methods that improve physiological and/or ecological selectivity. We have shown that simple adjustments in action thresholds for application of conventional insecticides against *B. tabaci* in cotton can reduce disruption of natural enemy populations (Naranjo et al., 2002). Commercial-scale field studies have also shown that management strategies based on the initial use of the IGRs buprofezin and pyriproxyfen preserves natural enemies compared with sole reliance on conventional insecticide

mixtures (Naranjo et al., 2003). Our results here confirm and augment these findings, and further quantify the selectivity of these IGRs relative to an untreated control.

We observed significant and immediate reductions in densities of most of the natural enemies examined over extended portions of the growing season with use of broad-spectrum, conventional insecticides. Conversely, the initial use of either buprofezin and pyriproxyfen for pest control conserved natural enemies, particularly arthropod predators. Nonetheless, densities of some predator taxa were reduced with use of the two IGRs in comparison with the untreated control. Densities of *C. carnea* s.l., *D.* nr. *divergens*, several spiders and coccinellids, the heteropteran predators *G. punctipes* and *N. alternatus*, and the omnivores *L. hesperus* and *S. albofasciatus* were significantly reduced under IGR regimes in at least one out of three years. In most instances, reductions in these taxa were much greater with use of conventional insecticides. Further, PRC analyses suggest that significant reductions in predator densities started many weeks after IGR applications. In 1997 reductions in the IGR regimes were associated with sprays of conventional insecticides in these regimes in early to mid-September (see Fig. 2A). However, only single applications of either buprofezin or pyriproxyfen were required in the IGR control regimes in 1998 and 1999 and reductions only occurred after 5 and 3 weeks, respectively (see Figs. 3A and 4A). These patterns suggest that reductions in predator populations may have been associated with more subtle and latent toxicological effects, and/or various indirect effects such as a reduction in prey density.

Field studies of insecticide effect on natural enemies integrate many factors, including direct toxicological effects and indirect effects such as reductions in prey availability. Direct toxicological effects of both IGRs have been shown in laboratory bioassays of various natural enemy species. Buprofezin reduced survival and prolonged development in first instar *C. rufilabris* (Burmeister) (Liu and Chen, 2000) and pyriproxyfen had similar effects on eggs and larvae (Chen and Liu, 2002). However, Balasubramani and Regupathy (1994) reported no effect of buprofezin on larval stages of *C. carnea*. Pyriproxyfen suppressed adult emergence of *Podisus maculiventris* (Say) (Declercq et al., 1995) and egg hatch in *Elatophilus hebraicus* Pericart (Mendel et al., 1994). Pyriproxyfen exposure in the nymphal stage caused some deformities in adult *G. punctipes*, but not *O. insidiosus* (Say), and no effects on reproduction were observed for either species (Naranjo and Prabhaker, unpublished). Likewise, Delbeke et al. (1997) and Nagai (1990) reported no effects of pyriproxyfen on several *Orius* spp. Buprofezin had no measurable effects on survival, molting or reproduction of *G. punctipes* or *O. insidiosus* (Naranjo and Prabhaker, unpublished). The most dramatic negative effects of these IGRs have been demonstrated for coccinellid beetles inhabiting perennial systems (Hattingh and Tate, 1995; Magagula and Samways, 2000; Mendel et al., 1994; Smith et al., 1999). Although coccinellids were rare at our study site, we observed no consistent negative effects of either IGR on these taxa.

Although direct toxicological effects of these IGRs cannot be dismissed, the relatively long interval (3–5 weeks) between application of either buprofezin or pyriproxyfen and reductions in predator populations suggests that other factors, such as reductions in prey density, may play a greater role. Many of the predators we examined are general feeders (van den Bosch and Hagen, 1966; Whitcomb and Bell, 1964), and *B. tabaci* is one of the most abundant arthropods occurring in our study area. Densities of *B. tabaci* nymphs were reduced soon after the application of either IGR, and egg and adult densities dropped within several weeks following applications. The gradual decline in predator populations in the IGR regimes relative to the untreated control over the season (see Figs. 2–4) was coincident with a similar decline in densities of whitefly prey. In contrast, immediate reductions in many predator taxa followed applications of conventional insecticides for whitefly suppression. The more consistent declines in *C. carnea* s.l., and *D.* nr. *divergens* in the IGR regimes may be related to the stronger affinity of these predators with whitefly prey. The empidid fly *D.* nr. *divergens sp.* was first discovered in association with large populations of *B. tabaci* in Arizona cotton and preliminary laboratory studies suggested that they could suppress adult *B. tabaci* and subsequent oviposition (Butler and Henneberry, 1993). Further laboratory feeding studies suggest that this species prefers to prey on adult *B. tabaci* (Hagler, 2002). *C. carnea* s.l. readily feeds on *B. tabaci* (Butler and Henneberry, 1988), and adult lacewings are known to be attracted to insect honeydews and artificial sugar supplements (e.g., Evans and Swallow, 1993; Hagen, 1986). Reductions in one of the most abundant prey in the system also may have increased opportunities for intraguild predation (Eubanks, 2001; Rosenheim et al., 1993) among predator species, further contributing to reductions in densities of some predators.

Rates of parasitism by aphelinid wasps were generally low, and neither the conventional nor IGR control regimes altered parasitism in a consistent manner. In contrast, a commercial-scale study showed that rates of parasitism were higher in fields sprayed with either buprofezin or pyriproxyfen compared with those sprayed with conventional insecticides (Naranjo et al., 2003). Field studies in Israel and southern California showed that rates of parasitism were unaffected by the use of broad-spectrum insecticides (Gerling and Naranjo, 1998). Because hosts must be present to measure parasitism, they suggested that insecticides affected

populations of both hosts and parasitoids equally, resulting in relatively stable levels of parasitism regardless of treatment. It is not clear that such a phenomenon was operating here as direct toxicological effects of the IGRs on parasitoids in laboratory bioassays is equivocal. Buprofezin caused mortality in early larval stages of *Encarsia luteola* Howard, *E. eremicus* and *E. tejanus* Rose and Zolnerowich (Gerling and Sinai, 1994; Hoddle et al., 2001; Jones et al., 1998), and pyriproxyfen reduced survival of young larvae of *E. eremicus* and *E. luteola* (Gerling and Sinai, 1994; Hoddle et al., 2001) and pupae of *E. formosa* Gahan (Liu and Stansly, 1997). However, buprofezin was benign to adults of several species of *Eretmocerus* and *Encarsia* (Hoddle et al., 2001; Jones et al., 1995) and pyriproxyfen was non-toxic to several species of *Encarsia* treated in the larval or adult stage (Liu and Stansly, 1997). Reductions in host density from insecticides may have influenced densities and/or searching behaviors of adult parasitoids leading to inconsistent changes in rates of parasitism. Lack of treatment differences could also be related to the relatively poor resolution provided by simple leaf samples for measuring parasitism (Naranjo, 2001). Finally, the relatively small size of plots in this study compared with those of Naranjo et al. (2003) may have facilitated interplot movement of adult parasitoids.

Although parasitoid to host ratios remained relatively consistent across treatments, higher ratios of predators to whitefly prey were generally observed with the use of IGRs compared with both the untreated control and the conventional control regime. Thus, even though use of the IGRs was associated with reductions in some predator populations, these materials were much more detrimental to whiteflies leading to predator:prey ratios more favorable to biological control. The tangible benefits of this conservation were not estimated directly in this study. However, in companion life table studies conducted in the same plots, we have shown that rates of natural enemy-induced mortality, primarily predation, on immature *B. tabaci* were significantly higher with the use of IGRs compared with conventional insecticides and this additional mortality contributed significantly to season-long suppression of *B. tabaci* in the IGR regimes (Naranjo, 2001; Naranjo and Ellsworth, unpublished). In addition, rates of predation in these life table studies were positively correlated with predator abundance, indicating that the level of conservation was directly related to pest mortality.

Cotton agroecosystems are characterized by multiple key pests. The use of transgenic cotton expressing *Bacillus thuringiensis* Berliner toxins in our study eliminated the need for additional insecticides for control of pink bollworm, *Pectinophora gossypiella* (Saunders) and other lepidopteran pests (Ellsworth and Jones, 2001). Although we evaluated *L. hesperus* as a non-target insect in terms of whitefly control, it is clear that this species remains a continual threat to cotton production in Arizona and California and there are currently no selective technologies for population suppression (Ellsworth, 2000). The addition of conventional insecticides for control of *L. hesperus* here dramatically reduced populations of many natural enemies. Although the lack of statistical interaction between whitefly and *L. hesperus* control regimes indicated that selectivity of the IGRs for whitefly control is realized even with the use of insecticides for *L. hesperus*, the overall benefits of this selectivity were diminished. In practice, these results emphasize the need to strictly follow available decision aids for *L. hesperus* suppression (Ellsworth, 2000). In research, our results highlight the importance of examining insecticide selectivity within the context of realistic pest management systems.

Buprofezin and pyriproxyfen are currently an integral component of pest management for *B. tabaci* in the western US, and their use is being widely adopted in Australian cotton where outbreaks of *B. tabaci* have recently occurred (Kelly et al., 2002). They are highly efficacious (Ellsworth and Naranjo, 1999; Ellsworth et al., 1998), their use delays or eliminates the need for conventional insecticides as part of an insecticide resistance management plan (Dennehy and Williams, 1997; Ellsworth et al., 1996a), and, as we have shown, they are highly selective. Pyriproxyfen and buprofezin were granted full registration in 1998 and 2002, respectively, and both materials are being widely used by producers in Arizona (Agnew and Baker, 2001; Agnew et al., 2000; Ellsworth and Martinez-Carrillo, 2001). The additional use of transgenic cotton further conserves natural enemy populations (Moar et al., 2002; Naranjo, 2002) thereby providing for selective control of two key pests. Since the introduction of these selective pest control methods in 1996, insecticide use in Arizona cotton declined nearly 85% from 1995 to 1999 (Ellsworth and Jones, 2001). In turn, this reduction in overall insecticide use in western cotton production systems is enabling true integrated control of *B. tabaci*, and may facilitate the further evolution of biologically based management of many pests founded on conservation and other approaches to biological control.

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