

# Quantifying Conservation Biological Control for Management of *Bemisia tabaci* (Hemiptera: Aleyrodidae) in Cotton

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## Abstract

Conservation biological control can be an effective tactic for minimizing insect-induced damage to agricultural production. In the Arizona cotton system, a suite of generalist arthropod predators provides critical regulation of *Bemisia tabaci* Gennadius (MEAM1) (Hemiptera: Aleyrodidae) and other pests. Arthropod predator and *B. tabaci* populations were manipulated with a range of broad-spectrum and selective insecticide exclusions to vary predator to prey interactions in a 2-yr field study. Predator to prey ratios associated with *B. tabaci* densities near the existing action threshold were estimated for six predator species found to be negatively associated with either adult and/or large nymphs of *B. tabaci* [*Misumenops celer* (Hentz) (Araneae: Thomisidae), *Drapetis* nr *divergens* (Diptera: Empididae), *Geocoris pallens* Stål (Hemiptera: Geocoridae), *Orius tristicolor* (White) (Hemiptera: Anthocoridae), *Chrysoperla carnea* s.l. (Neuroptera: Chrysopidae), and *Collops* spp. (Coleoptera: Melyridae)] with the first three most consistently associated with declining *B. tabaci* densities. Ratios ranged from 1 *M. celer* per 100 sweeps to 1 *B. tabaci* adult per leaf to 44 *D. nr. divergens* per 100 sweeps to 1 large nymph per leaf disk. These ratios represent biological control informed thresholds that might serve as simple-to-use decision tool for reducing risk in the current *B. tabaci* integrated pest management strategy. The identification of key predators within the large, flexible food web of the cotton agro-ecosystem and estimation of predator to *B. tabaci* ratios clarifies the role of key predators in *B. tabaci* suppression, yielding potential decision-making advantages that could contribute to further improving economic and environmental sustainability of insect management in the cotton system.

**Key words:** conservation biological control, predator to prey ratios, integrated pest management, biological control informed thresholds

Natural enemies have long been recognized as important to the regulation of herbivore populations (Hairston et al. 1960, Polis 1999) and can play a key role in management of insects in agricultural systems (van den Bosch and Messenger 1973). While the study of natural enemy/prey relationships has generally focused on interactions of single natural enemy species and single prey species, understanding communities and trophic levels can oftentimes be more appropriate for pest management in agricultural systems. The interactions of multiple natural enemy species can limit herbivores synergistically and facilitate pest suppression (Losey and Denno 1998). By altering prey behavior, multiple predators can synergistically increase or decrease total predation rates (Sih et al. 1998). Understanding natural enemy/prey

interactions can provide critical insight to pest suppression (Hassell and May 1986, Murdoch and Briggs 1996, Ives et al. 2005, Hallett et al. 2014), help to limit pest damage, and improve economic outcomes through conservation biological control (Naranjo et al. 2015).

Conservation biological control involves deliberate management practices that are used to favor existing natural enemies and enhance their ability to regulate pest populations. Such actions can involve maximizing habitat and resources through crop or landscape modification or reducing management pressures, such as through selective insecticide applications. Only rarely have there been specific integrations of conservation biological control into integrated pest management (IPM) systems via decision-making criteria (Hoffmann et al.

1990, Hamilton et al. 2004, Conway et al. 2006, Walker et al. 2010, Giles et al. 2017).

The sweetpotato whitefly, *Bemisia tabaci* Gennadius (MEAM1, Dinsdale et al. 2010) (Hemiptera: Aleyrodidae) is a key pest in the low desert cotton production system of the southwestern United States. While *B. tabaci* can reduce yields at elevated densities, lower densities can reduce lint quality by depositing honeydew excretions on open bolls, thereby promoting stickiness and the associated sooty mold complex that grows on these and other sugars (Ellsworth et al. 1999, Oliveira et al. 2001, Frisvold et al. 2007). In the Arizona system, an advanced IPM strategy has minimized losses from *B. tabaci* and dramatically reduced overall insecticide use (Ellsworth and Martinez-Carrillo 2001, Naranjo and Ellsworth 2009a) by guiding pest managers to regularly sample pest populations, use action thresholds and deploy selective insecticides when control actions are needed (Ellsworth et al. 2006).

A suite of arthropod predators prey on *B. tabaci* (Hagler 2002, Hagler et al. 2004, Hagler and Naranjo 2005) and are a primary source of mortality to *B. tabaci* in the field (Naranjo and Ellsworth 2005, 2009b). This complex of natural enemies exists as a food web often feeding and preying upon alternative prey including each other. Natural enemy conservation is currently promoted through the use and timing of selective insecticides that are safer to the natural enemy community. However, decision-making remains pest-centric and based solely on measurement of pest densities (Ellsworth et al. 2006, Naranjo and Ellsworth 2009a). Action thresholds for *B. tabaci* are based on the sampling of multiple life stages and applied variously according to population development. While this approach is not static, it is subject to errors in decision-making because of unmeasured or unincorporated variables in *B. tabaci* population development that influence rates of growth. Taking into account control provided by arthropod predators is a refinement that could improve conservation biological control of *B. tabaci* by allowing pest managers to make more informed control decisions.

To better understand effects of the complex of arthropod predators on *B. tabaci* population dynamics in the cotton production system, we used insecticidal manipulations to establish varying densities of predator and *B. tabaci* populations. We then identified key predators within the natural enemy community that may suppress *B. tabaci* populations and estimated predator to *B. tabaci* ratios to reduce uncertainty in decision-making. Such biological control informed thresholds would be relevant during critical periods of active decision-making by pest managers (i.e., perithreshold) and could improve decisions for insecticidal interventions through the integration of chemical and biological control tactics.

## Materials and Methods

### Experimental Setup

Studies were conducted at the University of Arizona's Maricopa Agricultural Center, Maricopa, AZ, in 2011 and 2012. A common Bollgard II / Roundup Ready Flex cotton variety (Monsanto Company, St. Louis, MO) that confers resistance to lepidopteran insects and glyphosate was used each year (DP1032B2RF). The cotton was planted on 5 May 2011 and 15 May 2012. To insure a sufficient supply of *B. tabaci* to our system, cantaloupe and watermelon were planted 3 to 1 (Jumbo Hales Best and Crimson Sweet, respectively) in proximity to the cotton, emulating a common cropping system in Arizona. In 2011, melons were planted in four row strips bordering the west and east edges of the cotton and in the middle of the experimental area. In 2012, the melons ran in four row strips along the east and west borders of each plot. Melons were irrigated at the same time as the cotton and were dried down slowly

in the middle of July (concurrent with insecticide treatments, see Insecticide Exclusion below) to allow *B. tabaci* to gradually move into the adjacent cotton. All crops were grown according to standard agronomic practices for the area and yields were assessed to ensure that they fell within a commercially acceptable range for the region.

A randomized complete block design with four replicates was used in both years with arthropod predator and *B. tabaci* manipulations as the treatments. In 2011, there were nine insecticidal exclusion treatments replicated four times for a total of 36 plots. One treatment did not reach sufficient *B. tabaci* levels for insecticide exclusion and was considered a duplicate untreated control (UTC). Plots were 22.9-m long and 24 rows (24.4 m) wide with 4-m alleys. In 2012, there were 12 insecticidal exclusion treatments replicated four times for a total of 48 plots. Plots were 21.9-m long and 24 rows (24.4 m) wide with 3.7-m alleys. Unmanaged cotton borders were 17.1 m (2011) and 7.6–9.1 m (2012) and ran the full width, north and south, of the experimental area.

### Insecticide Exclusion

Each insecticide exclusion treatment was applied to intentionally reduce *B. tabaci* and/or arthropod predator populations to varying degrees (Table 1). The broad-spectrum insecticide acephate is known to reduce natural enemies while on its own having minimal effects on *B. tabaci* (Asiimwe et al. 2013). The selective insecticides pyriproxyfen and buprofezin reduce *B. tabaci* populations but have minimal effects on natural enemy populations (Palumbo et al. 2001, Naranjo et al. 2004). A fenpropathrin + acephate mixture was applied to suppress both *B. tabaci* and natural enemy populations. In 2012, the acaricide etoxazole was applied in select insecticide exclusion treatments to ensure that resurgent two spotted spider mites, *Tetranychus urticae* (Koch) (Acari: Tetranychidae), did not interfere with *B. tabaci* population or crop development. Sprays were made mid-summer on 12 and 29 July 2011, and 11 July, 25 July, and 6 August 2012, except for threshold-timed sprays of pyriproxyfen and buprofezin on 11 and 31 August 2012, respectively.

### *B. tabaci* and Arthropod Predator Sampling

*B. tabaci* populations were sampled weekly as described by Naranjo and Flint (1994, 1995) in a manner compatible with current pest manager field practices (Ellsworth et al. 2006). Five *B. tabaci* adult samples (undersides of fifth main-stem leaves from the terminal) and 10 *B. tabaci* large nymph samples (3.88-cm<sup>2</sup> disk between the main and left lateral leaf vein on the abaxial side of fifth main-stem leaves) were collected weekly from each plot over 5 wk in 2011 and 7 wk in 2012. *B. tabaci* immature life stages were enumerated as eggs, small nymphs (first and second instars) and large nymphs (third and fourth instars, inclusive of pharate adults or 'pupae'). These large nymphs, which are the recommended preimaginal life stage sampled for management (Ellsworth et al. 2006), are the only immature life stage considered hereafter.

Arthropod predator densities were sampled with a 38-cm diameter sweep net. Fifty sweeps (two 25-sweep subsamples through the top of the canopy) were taken from each plot. Sweeps were collected on a weekly basis, concurrent with *B. tabaci* sampling. Samples were immediately bagged, frozen, and later examined for arthropod predators; 14 taxa were consistently found in sufficient numbers for analyses. Aphelinid *B. tabaci* parasitoids were not sampled because previous life-table studies suggest that parasitoids contribute little mortality to *B. tabaci* relative to generalist predators in this system (Naranjo and Ellsworth 2005).

### Management of *B. tabaci* and Other Pests

Elevated populations of *Lygus hesperus* Knight (Hemiptera: Miridae) severely reduce cotton yield and affect plant growth (Leigh

**Table 1.** Insecticide exclusion treatments applied to cotton to establish contrasted conditions by manipulating predator and *B. tabaci* prey densities to varying degrees, Maricopa, AZ. See text for spray dates.

Insecticide exclusion treatment (g A.I./ha)	Intended predator reduction	Intended <i>B. tabaci</i> reduction	2011 Sprays	2012 Sprays
Acephate (1123) <sup>a</sup>	Very large	None	2	3 <sup>b</sup>
Acephate (561.5) <sup>a</sup>	Large	None	2	3
Acephate (280.75) <sup>a</sup>	Moderate	None	N/A	3
Acephate (112.3) <sup>a</sup>	Slight	None	2	3
Acephate (11.23) <sup>a</sup>	Very slight	None	2	3
Fenprothrin (224.6) <sup>c</sup> + acephate (561.5) <sup>a</sup>	Large	Moderate	2	3
Acetamiprid (112.3) <sup>d</sup>	Small	Large	2	3 <sup>b</sup>
Pyriproxyfen (60.64) <sup>e</sup> then buprofezin (393.05) <sup>f</sup>	None	Large	2	2
<sup>g</sup> Pyriproxyfen (60.64) <sup>e</sup> then buprofezin (393.05) <sup>f</sup>	None	Large	N/A	2
UTC	None	None	N/A	N/A

<sup>a</sup>Orthene 97, AMVAC, Newport Beach, CA.

<sup>b</sup>Zeal WDG, Valent, Walnut Creek, CA, added at 22.46 g A.I./ha for prophylactic control of mites.

<sup>c</sup>Danitol 2.4 EC, Valent, Walnut Creek, CA.

<sup>d</sup>Intruder 70 WSP, Gowan, Yuma, AZ.

<sup>e</sup>Knack, Valent, Walnut Creek, CA.

<sup>f</sup>Courier SC, Nichino America, Inc., Wilmington, DE.

<sup>g</sup>Treated after reaching existing action threshold.

et al. 1998, Ellsworth and Barkley 2001). To minimize these effects, *L. hesperus* populations were sampled concurrently with arthropod predators (from sweep samples described above) and counted in real time. When *L. hesperus* populations exceeded the action threshold (15 total insects with at least 4 nymphs per 100 sweeps, Ellsworth and Barkley 2001), the entire experiment was treated with flonicamid at a rate of 16.1 g A.I./ha, a selective insecticide which has minimal impact on *B. tabaci* or natural enemies in this system (Naranjo and Ellsworth 2009a). Some studies suggest low efficacy of flonicamid on *B. tabaci* at much higher application rates (Roditakis et al. 2014). Nonetheless, the goal was to differentially manipulate whitefly and predator densities and the experiment-wide application of flonicamid had no bearing on this outcome. When *B. tabaci* large nymph and adult populations reached established action thresholds (three adults per leaf and one large nymph per leaf disk, (Naranjo et al. 1998, Ellsworth et al. 2006), selective insecticides were applied at recommended rates (Ellsworth et al. 2006). Spiromesifen (280.75 g A.I./ha) was used in 2011 and buprofezin (393.05 g A.I./ha) in 2012.

## Statistical Analysis

### Identifying Insecticide Exclusion Effects

A mixed-model ANOVA (JMP V9, SAS Institute Inc., Cary, NC) was used to identify factors affecting *B. tabaci* densities each year, including fixed effects of sampling date and insecticide exclusion treatments. Block and associated interaction terms were considered random effects. *B. tabaci* seasonal mean densities were compared with a Tukey–Kramer HSD test. Because additional insecticide exclusion chemistries and applications were used in 2012, separate analyses were also performed for each year. Similar mixed-model ANOVAs were used to identify the effects of insecticidal exclusion on yield (kg lint/ha) each year.

The effects of insecticide exclusion on arthropod predator densities were subjected to principal response curve (PRC) analysis in CANOCO 5 (Ter Braak and Šmilauer 2012). PRC is a multivariate, time-dependent analysis (Van den Brink and Ter Braak 1998, 1999) that depicts the arthropod community response to treatments over time. Canonical coefficients link species' densities together on a common scale to a reference, which in this case was an UTC.

Species weights denote the relationship of a particular species to the time-dependent pattern of the canonical coefficients. Species with weights greater than 0.5 have a response that is more closely associated to the patterns expressed by PRCs. Species with values less than -0.5 are also influential but with responses opposite to the pattern expressed by the PRCs. Species with weights between -0.5 and 0.5 are less influential and of less interest. Significance of each insecticide manipulation was estimated by permutation-based *F*-tests.

### Identifying Key Candidate Predators

Predator to *B. tabaci* ratios for 14 predator taxa were assessed via multiple and logistic regression analysis for each year to identify ratios significantly associated with *B. tabaci* abundance. Taxa for which a significant negative association between predator to *B. tabaci* ratios and *B. tabaci* abundance was observed were putatively identified as key predators that could be useful for *B. tabaci* control decision making. In multiple regression analyses, the response variable was the ln-transformed mean *B. tabaci* densities (adults or large nymphs), and explanatory variables were the ln-transformed predator to *B. tabaci* ratios and the categorical fixed effects of insecticidal exclusion treatment and sampling date. In logistic regression analyses, the response variable was the proportion of leaves or leaf disks with *B. tabaci* densities exceeding the thresholds (i.e., a binomial count), and explanatory variables were the ln-transformed predator to *B. tabaci* ratios and the categorical fixed effects of insecticidal exclusion treatment and sampling date. To reduce in calculable values and achieve requirements for normality and homogeneity of variance, predator to *B. tabaci* ratios were transformed as  $\ln(A/(B + 0.1) + 1)$ , where *A* is the mean density of an arthropod predator per 100 sweeps and *B* is the mean density of *B. tabaci* adults per leaf or *B. tabaci* large nymphs per leaf disk. Action thresholds were expressed as the frequency of sampled leaves or leaf disks with numbers of *B. tabaci* nymphs or adults exceeding a certain density ( $\geq 3$  adults or  $\geq 1$  large nymph, Ellsworth et al. 2006). For each analysis, a model with all variables was first fitted to identify significant effects and nonsignificant terms were removed to produce a parsimonious inferential model.

### Assessing Candidate Predator Interactions

Predator interactions that might interfere with *B. tabaci* suppression (e.g., by intraguild predation or other antagonistic behaviors) were

examined via multiple regression. The response variable was the ln-transformed mean *B. tabaci* density (adults or large nymphs), and explanatory variables included insecticidal exclusion treatment and sampling date as fixed effects and transformed predator to *B. tabaci* ratios of key predators and all two-way predator interactions as covariates. In these analyses, significant interactions involving two predators may indicate antagonistic or synergistic effects between the predators.

### Determining Critical Values for Ratios

Simple linear regressions of ln-transformed predator to *B. tabaci* ratios (explanatory variable) on *B. tabaci* densities (response variable) were used to estimate ratio values and 95% CIs that correspond to the *B. tabaci* action thresholds of three adults per leaf and one large nymph per leaf disk each year. These estimated ratios were contrasted with ratios calculated from multiple regression to account for the effects of other key predators. Inverse prediction was used for simple, multiple and logistic regression models (Ramsey and Shafer 2002) to identify the ratio and 95% CIs of key predators that corresponded to the *B. tabaci* action threshold each year. The response variable was the ln-transformed mean *B. tabaci* density (adults or large nymphs).

The ratios calculated from simple and multiple regressions were then optimized by assessing the practical implications of decision-making. In this optimization, the recommendations for *B. tabaci* control sprays based on estimated ratios were compared with recommendations for *B. tabaci* control sprays based on the *B. tabaci* only action threshold over both years. Instances where ratio-based recommendations diverged from the pest-centric action threshold were identified as either ‘early’- or ‘late’-spray disagreements (advancing insecticide intervention due to lower predator to prey ratios, or deferring insecticide intervention due to elevated predator

ratios, respectively). A graphical approach was used to examine the rates of disagreement for the range of ratios encompassed by simple and multiple regression. Predator to prey ratios that resulted in the lowest total rate of disagreement (‘early’ sprays + ‘late’ sprays) were considered optimal from a decision-making perspective.

## Results

### Insecticide Exclusion Effects

Insecticide exclusions deployed to alter *B. tabaci* and predator abundance followed patterns and confirmed effects intended by design (Table 1). Broad-spectrum acephate treatments generally resulted in higher *B. tabaci* densities compared with the UTC in both years, with lessening effects corresponding to reduced application rates of this material. Selective insecticide exclusions were associated with lowered *B. tabaci* densities, likely due to their target efficacy and the associated conservation of natural enemies (Fig. 1). *B. tabaci* adult densities were significantly affected by insecticide exclusion treatment ( $F = 5.4$ ,  $df = 7, 20.5$ ,  $P < 0.0001$ ) and sampling date ( $F = 30.9$ ,  $df = 4, 12.9$ ,  $P = 0.001$ ) in 2011, while large nymph densities were significantly affected by insecticide exclusion ( $F = 8.9$ ,  $df = 7, 7.3$ ,  $P = 0.004$ ) but not by sampling date ( $P > 0.05$ ) (Fig. 1). In 2012, *B. tabaci* adult densities were significantly affected by insecticide exclusion ( $F = 10.1$ ,  $df = 11, 33.9$ ,  $P < 0.0001$ ) and sampling date ( $F = 39.3$ ,  $df = 7, 20.9$ ,  $P < 0.0001$ ), as were large nymph densities (insecticide exclusion:  $F = 18.7$ ,  $df = 11, 33.4$ ,  $P < 0.0001$ ; sampling date:  $F = 28.2$ ,  $df = 7, 21.1$ ,  $P < 0.0001$ ) (Fig. 1).

PRC analysis demonstrated expected effects of insecticide exclusion on predator abundance through time in 2011 ( $F = 36.9$ ,  $P = 0.002$ ) from the first axis of redundancy analysis, which explained 53.3% of the variation. In 2012, the exclusion effect was again

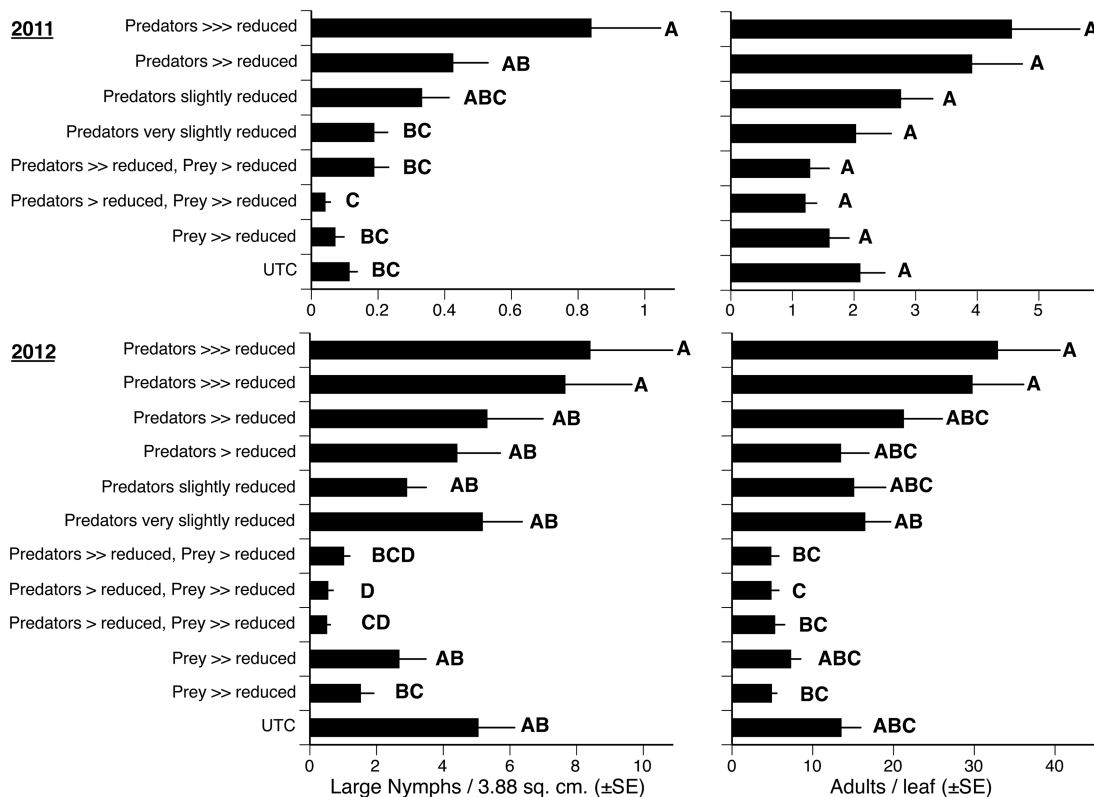


Fig. 1. Insecticide exclusion manipulation effects on postspray seasonal mean densities of *B. tabaci* large nymphs and adults ( $\pm$ SE) in Maricopa, AZ. See Table 1 for intended reduction effects. Means not sharing a letter are significantly different from each other ( $P < 0.05$ , Tukey–Kramer HSD).

significant ( $F = 32.4, P = 0.002$ ) from the first axis of redundancy analysis, which explained 35.4% of the variation. Generally, broad-spectrum insecticidal exclusion (e.g., various rates of acephate) had a very large effect on predator populations in both years and significantly reduced populations below the reference UTC; smaller reductions in predator populations were also apparent where acetamiprid was deployed (Fig. 2). Predator abundance in the selective insecticide treatments, such as pyriproxyfen, was not different from the UTC.

The relative contribution of each species within the natural enemy community is denoted by species weights, with higher weights (>0.5) indicating greater correspondence to the general community pattern depicted by the PRC. Nine predator taxa followed the general pattern depicted by the PRC in 2011, while four of these same taxa followed the PRC pattern in 2012 (Fig. 2). Two predator taxa followed a numerical trend opposite to the general community pattern depicted by the PRC suggesting they are also influential, but following a numerical trend opposite to that depicted in the PRC (i.e., a sign change). Three remaining taxa did not follow the PRC pattern either year.

**Identifying Key Candidate Predators**

*Multiple Regression Analysis of B. tabaci Population Density*

In 2011, sampling date was significantly associated with *B. tabaci* adult density ( $F = 3.4, df = 4, 17, P = 0.032$ ), but insecticide exclusion treatment was not ( $P = 0.10$ ). No predator to *B. tabaci* ratios were significantly associated with *B. tabaci* adult densities this year ( $P \geq 0.10$ , Table 2). Insecticide exclusion treatment was significantly

associated with *B. tabaci* nymph density in 2011 ( $F = 3.2, df = 7, 14, P = 0.029$ ) but sampling date was not ( $P = 0.11$ ). In the model including only the effects of insecticide exclusion treatment, the ratio of adult *Collops* spp. (Coleoptera: Melyridae) was significantly negatively associated with large nymph density (Table 2).

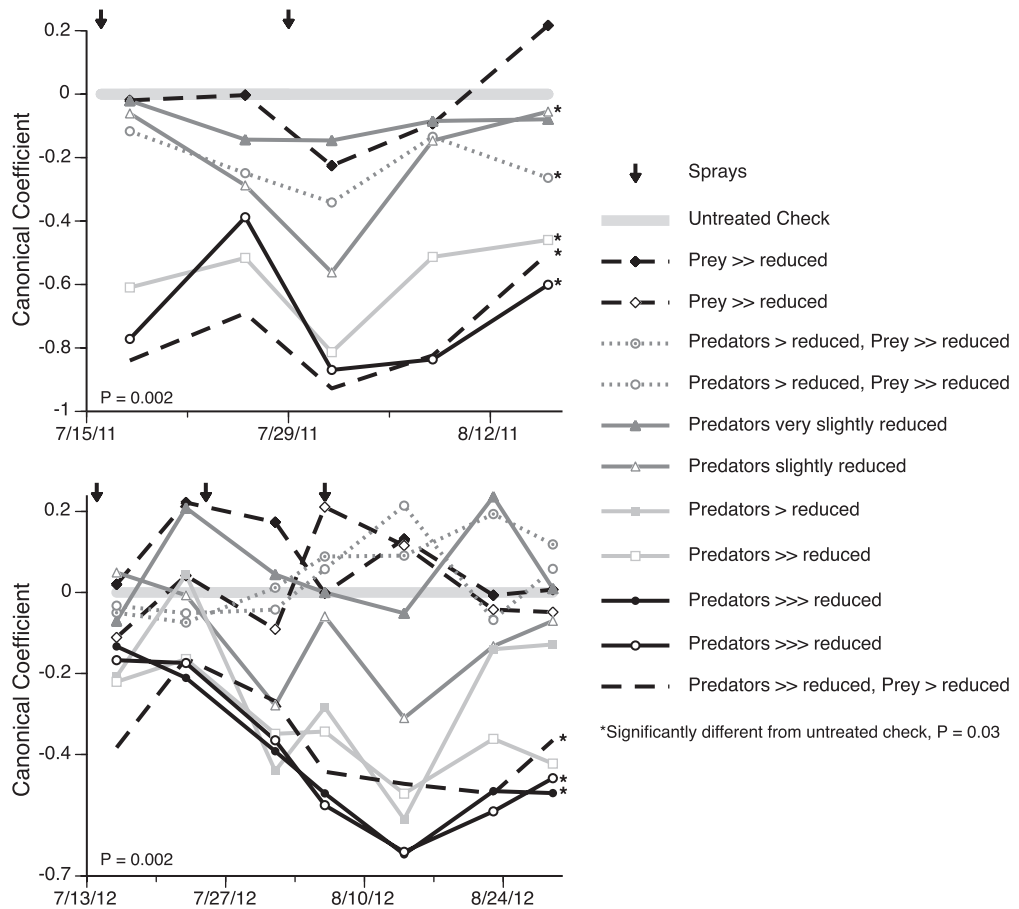
In 2012, sampling date was significantly associated with *B. tabaci* adult density ( $F = 7.8, df = 7, 52, P < 0.0001$ ), but insecticide exclusion treatment was not ( $P = 0.86$ ). In the model including effects of sampling date, the ratios for pooled adult and juvenile *Misumenops celer* (Hentz) (Araneae: Thomisidae) and adult *Drapetis nr divergens* (Diptera: Empididae) were significantly negatively associated with adult density (Table 2). Both insecticide exclusion treatment ( $F = 2.1, df = 11, 52, P = 0.033$ ) and sampling date ( $F = 18.4, df = 7, 52, P < 0.0001$ ) were significantly associated with nymph density. In the model incorporating these effects, the ratios for *M. celer*, *D. nr divergens*, and pooled adult and nymphal *Geocoris pallens* Stål (Hemiptera: Geocoridae) were significantly negatively associated with nymph density (Table 2).

*Logistic Regression Analyses of Proportions of Leaves or Leaf Disks Exceeding Threshold Density*

In 2011, neither sampling date ( $P = 0.18$ ) nor insecticide exclusion treatment ( $P = 0.49$ ) were significantly associated with the proportion of leaves exceeding threshold for *B. tabaci* adults. Ratios for *M. celer*, *D. nr divergens*, and larval *Chrysoperla carnea* s.l. (Neuroptera: Chrysopidae) were significantly negatively associated

Species	Weight
<i>M. celer</i>	2.32
<i>G. punctipes</i>	1.55
<i>D. nr. divergens</i>	1.09
<i>O. tricolor</i>	1.08
<i>G. pallens</i>	1.04
<i>Collops</i> spp.	0.91
<i>N. alternatus</i>	0.64
<i>Z. renardii</i>	0.60
All other spiders	0.55
<i>R. forticornis</i>	0.40
<i>S. albofasciatus</i>	0.20
<i>H. convergens</i>	0.19
All other coccinellids	0.17
<i>C. carnea</i> larvae	-0.74

Species	Weight
<i>M. celer</i>	2.14
<i>Z. renardii</i>	1.54
<i>G. punctipes</i>	1.28
All other spiders	0.71
<i>O. tricolor</i>	0.42
<i>N. alternatus</i>	0.29
<i>G. pallens</i>	0.21
<i>Collops</i> spp.	0.04
<i>R. forticornis</i>	0.01
<i>S. albofasciatus</i>	-0.10
<i>D. nr. divergens</i>	-0.11
All other coccinellids	-0.16
<i>H. convergens</i>	-0.77
<i>C. carnea</i> larvae	-1.99



**Fig. 2.** Insecticide exclusion manipulation effects on arthropod predator communities based on PRC analyses compared to the untreated control ( $\gamma = 0$ ). The product of the species weight and the canonical coefficient for a given insecticidal manipulation and time estimates the natural log change in density of that species relative to the untreated control. Key predators with species weights greater than 0.5 and less than -0.5 are indicated in bold.

with the proportion of leaves exceeding threshold densities (Table 3). In 2011, insecticide exclusion, but not sampling date ( $P = 0.37$ ) treatment, was significantly associated with the proportion of leaf disks exceeding threshold for *B. tabaci* nymphs ( $\chi^2=22.94$ ,  $df = 7, 19$ ,  $P = 0.001$ ). Infestation rate of *B. tabaci* nymphs was not significantly associated with any predator to *B. tabaci* ratios (Table 3).

In 2012, the effect of sampling date, but not insecticide exclusion ( $P = 0.33$ ), was significantly associated with *B. tabaci* adult infestation rate ( $\chi^2=22.3$ ,  $df = 7, 52$ ,  $P = 0.002$ ). After excluding insecticide treatment, the ratios of *D. nr divergens* and pooled adult and nymphal *Orius tristicolor* (White) (Hemiptera: Anthocoridae) were significantly negatively associated with adult infestation rates (Table 3). The effect of insecticide exclusion treatment was significantly associated with *B. tabaci* nymph infestation rate ( $\chi^2 = 33.3$ ,  $df = 11, 52$ ,  $P = 0.0005$ ), as was sampling date ( $\chi^2 = 51.9$ ,  $df = 7, 52$ ,  $P < 0.0001$ ). Including these effects, the ratio of *D. nr divergens* and *G. pallens* were significantly negatively associated with nymph infestation rates (Table 3).

In summary, the analyses indicated that the ratios of six predator taxa (*M. celer*, *D. nr divergens*, *G. pallens*, *O. tristicolor*, *C. carnea*, and *Collops* spp.) to various *B. tabaci* densities were negatively associated with *B. tabaci* abundance or infestation rates, suggesting that these predators may actively regulate *B. tabaci* populations. *M. celer*, *D. nr divergens*, and *G. pallens* were found to be negatively associated with *B. tabaci* densities and infestation through multiple analytical approaches, suggesting more reliable relationships.

The ratio of two predators, *Rhinacloa forticornis* (Reuter) (Hemiptera: Miridae) and *Collops* spp., to prey were positively associated with infestation rate of nymphs in 2012, suggesting that these predators benefit from feeding on *B. tabaci* nymphs without regulating nymph infestations, or that they are involved in intra-guild interactions that interfere with nymph control provided by other

predators. The ratios of many other predators were not significantly associated with abundance or infestation rate of *B. tabaci* [i.e., *Zelus renardii* (Hemiptera: Reduviidae), *Hippodamia convergens* (Guérin-Méneville) (Coleoptera: Coccinellidae), *Spanogonicus albofasciatus* (Reuter) (Hemiptera: Miridae), *Nabis alternatus* (Parshley) (Hemiptera: Nabidae), *Geocoris punctipes* (Say) (Hemiptera: Geocoridae), a synthetic group of all spiders (Araneae) excluding *M. celer*, and a synthetic grouping of all Coccinellids excluding *H. convergens*].

### Assessing Candidate Predator Interactions

In 2012, one predator interaction effect was positively associated with *B. tabaci* adult densities indicating an antagonistic interaction ( $F = 180.5$ ,  $df = 21, 62$ ,  $P < 0.0001$ ): *M. celer* \* *D. nr divergens* ( $F = 26.9$ ,  $df = 1, 62$ ,  $P < 0.0001$ ). Sampling date, but not insecticide exclusion treatment ( $P = 0.31$ ), was significantly associated with adult *B. tabaci* densities ( $F = 52.2$ ,  $df = 7, 62$ ,  $P < 0.0001$ ) and was incorporated in the model. One predator interaction was negatively associated with nymph densities, indicating a synergistic interaction, in 2012 ( $F = 165.9$ ,  $df = 25, 58$ ,  $P < 0.0001$ ): *M. celer* \* *G. pallens* ( $F = 5.3$ ,  $df = 1, 58$ ,  $P = 0.025$ ). Again, sampling date ( $F = 45.3$ ,  $df = 7, 58$ ,  $P < 0.0001$ ), but not insecticide exclusion ( $P = 0.07$ ), was included in the model.

One predator interaction effect was negatively associated with *B. tabaci* adult infestation in 2012 ( $\chi^2=826$ ,  $df = 25, 58$ ,  $P < 0.0001$ ): *M. celer* \* *D. nr divergens* \* *O. tristicolor* ( $F = 4.24$ ,  $df = 1, 58$ ,  $P = 0.039$ ). Sampling date ( $F = 47.4$ ,  $df = 7, 58$ ,  $P < 0.0001$ ), but not insecticide exclusion ( $P = 0.24$ ), was included in the model. One predator interaction effect was negatively associated with nymph infestation in 2012 ( $\chi^2=1121$ ,  $df = 33, 50$ ,  $P < 0.0001$ ): *D. nr divergens* \* *R. forticornis* \* *G. pallens*. Both sampling date and insecticidal treatment were significantly associated with nymphal

**Table 2.** Predator to *B. tabaci* ratios that were significantly associated to *B. tabaci* densities by multiple regression in 2011 and 2012.

Predator to <i>B. tabaci</i> ratio <sup>a</sup>	Year	Coefficient	SE	F-ratio	Df	P-value	R <sup>2</sup>
<i>Collops</i> spp. to nymphs	2011	-0.56	0.11	15.4	1, 31	<0.01	0.98
<i>D. nr divergens</i> to adults	2012	-0.95	0.05	170.6	1, 75	<0.01	0.62
<i>D. nr divergens</i> to nymphs	2012	-0.78	0.07	147.8	1, 63	<0.01	0.98
<i>G. pallens</i> to nymphs	2012	-0.17	0.06	9.1	1, 63	<0.01	0.98
<i>M. celer</i> to adults	2012	-0.33	0.09	6.5	1, 75	0.01	0.62
<i>M. celer</i> to nymphs	2012	-0.23	0.07	10.6	1, 63	<0.01	0.98

<sup>a</sup>Regression statistics are associated with the individual variable noted; R<sup>2</sup> is for the full model. Multiple regression identified no predators significantly associated with *B. tabaci* adult densities in 2011.

**Table 3.** Predator to *B. tabaci* ratios that were significantly associated to *B. tabaci* densities by logistic regression in 2011 and 2012.

Predator to <i>B. tabaci</i> ratio <sup>a</sup>	Year	Coefficient	SE	$\chi^2$	df	P-value
<i>C. carnea</i> to adults	2011	-0.74	0.19	25.5	1, 41	<0.01
<i>D. nr divergens</i> to adults	2011	-1.03	0.11	153.4	1, 41	<0.01
<i>M. celer</i> to adults	2011	-0.75	0.12	7.7	1, 41	<0.01
<i>Collops</i> spp. to nymphs	2012	0.23	0.16	4.1	1, 61	0.04
<i>D. nr divergens</i> to adults	2012	-1.38	0.10	83.5	1, 75	<0.01
<i>D. nr divergens</i> to nymphs	2012	-0.69	0.09	20	1, 61	<0.01
<i>G. pallens</i> to nymphs	2012	-0.27	0.12	5.6	1, 61	0.02
<i>O. tristicolor</i> to adults	2012	-0.54	0.27	4.1	1, 75	0.04
<i>R. forticornis</i> to nymphs	2012	0.34	0.14	5.8	1, 61	0.02

Note: The response variable was the proportion of leaves (adults) or leaf disks (nymphs), where *B. tabaci* infestations (binomial count) exceeded existing action thresholds.

<sup>a</sup>Regression statistics are associated with the individual variable noted. Logistic regression identified no predators significantly associated with *B. tabaci* nymph infestations in 2011.

infestation ( $\chi^2=28.2$ ,  $df = 7$ ,  $50$ ,  $P < 0.0001$ , and  $\chi^2=39.7$ ,  $df = 11$ ,  $50$ ,  $P < 0.0001$ , respectively).

### Determining Critical Values for Ratios

For each of the six predators that may have contributed to regulating *B. tabaci* populations (Tables 2 and 3), we estimated the predator ratio that corresponds to the current *B. tabaci* action threshold from simple linear regressions (Fig. 3, Supp Table 1 [online only]), and multiple or logistic regressions (i.e., biological control informed thresholds). The range of estimated ratios from these two methods was then optimized so as to minimize mistimed spray decisions relative to the conventional *B. tabaci* action threshold (i.e., optimized spray decisions that minimize decision error rates, Fig. 4). In general, these biological control informed thresholds estimated with multiple or logistic regression varied from those obtained with simple linear

regression (Fig. 5, Supp Table 2 [online only]), an expectation if population density of some predators that collectively affect *B. tabaci* populations are correlated.

### Discussion

In many insect management systems, conservation biological control is often arguably treated as a passive tactic that emerges as a result of not spraying broad-spectrum insecticides. Little else guides its utility in IPM. In contrast, decision-support systems for understanding and acting on target pest population dynamics are generally substantially supported through research and grower educational activities. One reason for this investment deficit is the ecological complexity of the conserved natural enemies in most field cropping systems. Our study sought to uncover those

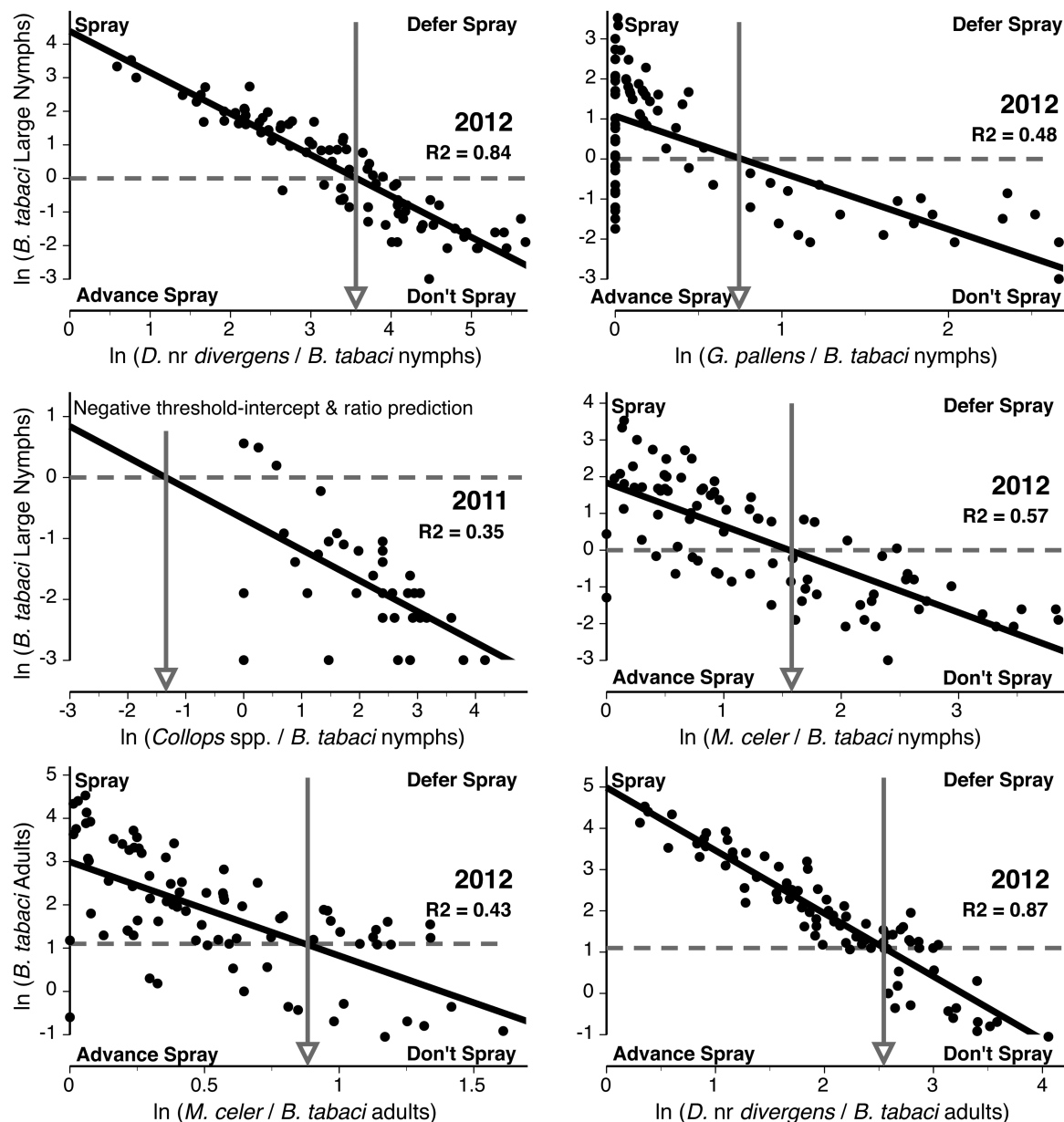


Fig. 3. Regressions of *B. tabaci* density or *B. tabaci* percent infestation on predator to prey ratios in years that key predators were associated with *B. tabaci* suppression. *B. tabaci* density is expressed as  $\ln$  (adults per leaf) or  $\ln$  (large nymphs per 3.88 cm<sup>2</sup> leaf disc). Proposed  $\ln$  (ratios) (arrows) are estimated from the intersection of the regression line and the existing *B. tabaci* action threshold (dotted lines). Spray decision zones are indicated from the four resulting quadrants.

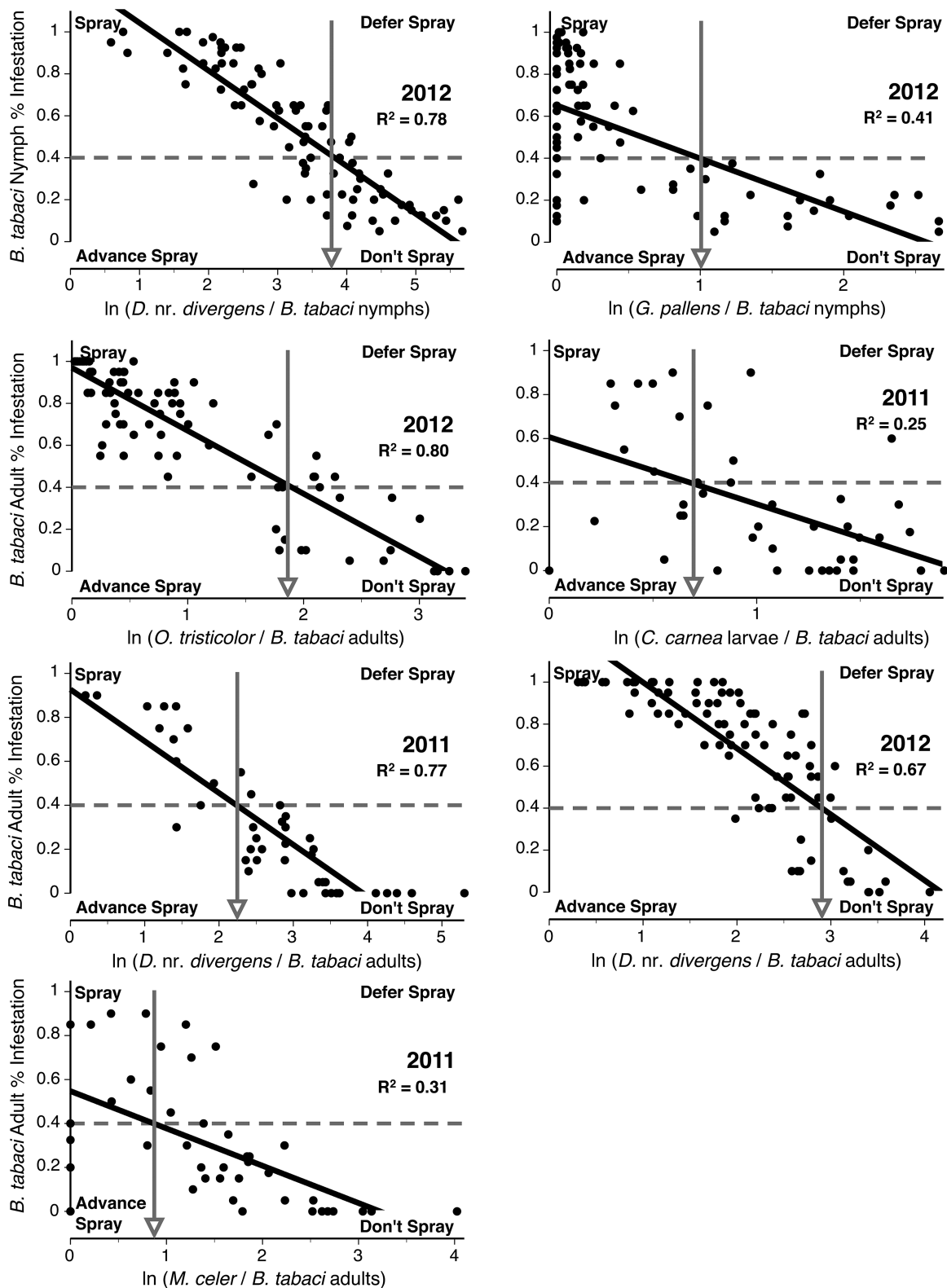
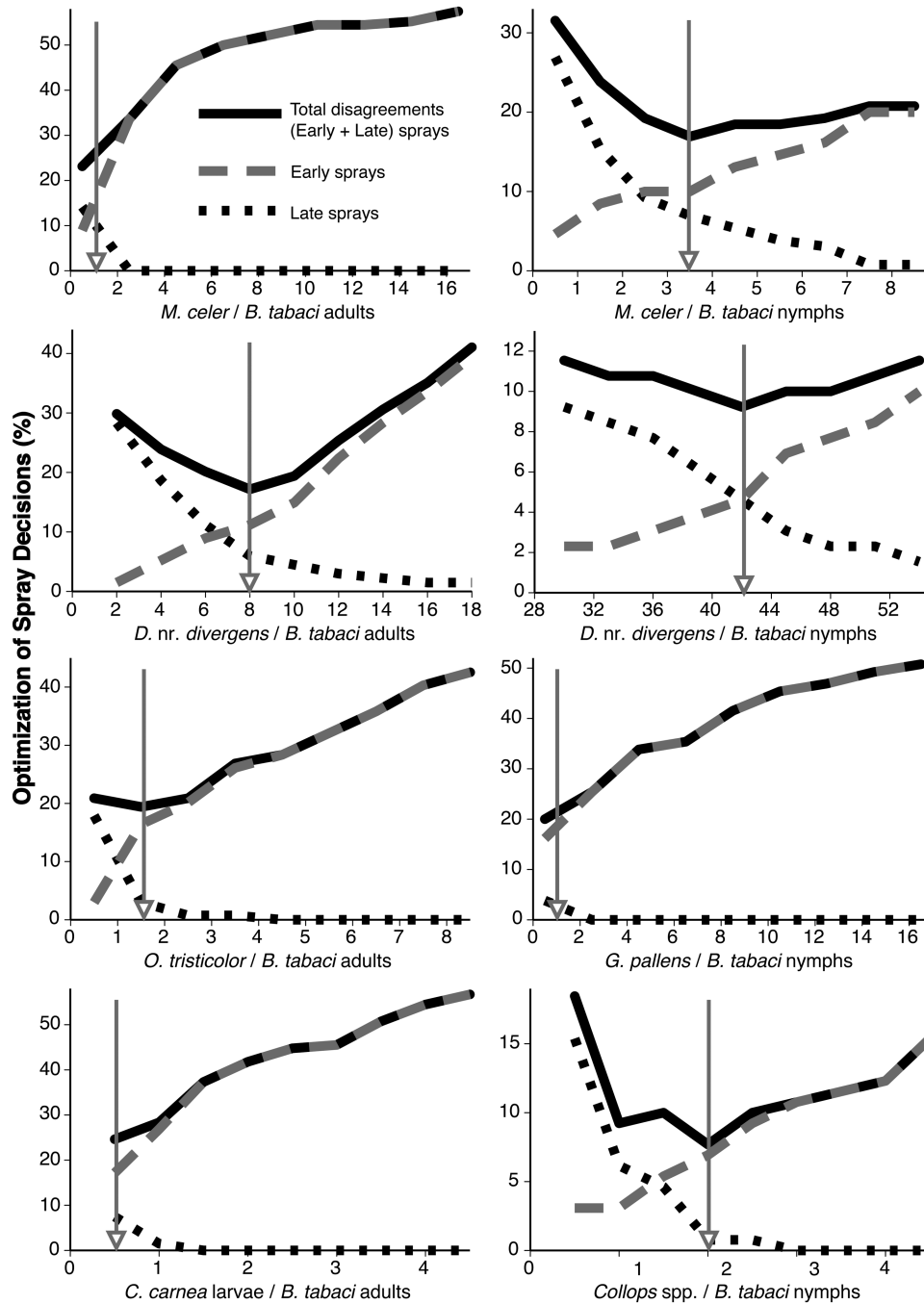


Fig. 3. Continued

relationships most related to the suppression of *B. tabaci*, a key pest of cotton in the desert Southwest. Six taxa, all generalist predators, were identified as potential biological control agents present in this agroecosystem. Furthermore, in each case, a predator to prey ratio was proposed as a means for interpreting the function of biological control, potentially useful in decision support when

the target pest is around the standard threshold, i.e., perithreshold. These food web relationships were tested within the context of insecticides commonly used in commercial cotton systems. Thus, there is high likelihood, that with further research, growers will be able to defer or advance *B. tabaci* sprays based on the predicted function of conservation biological control.

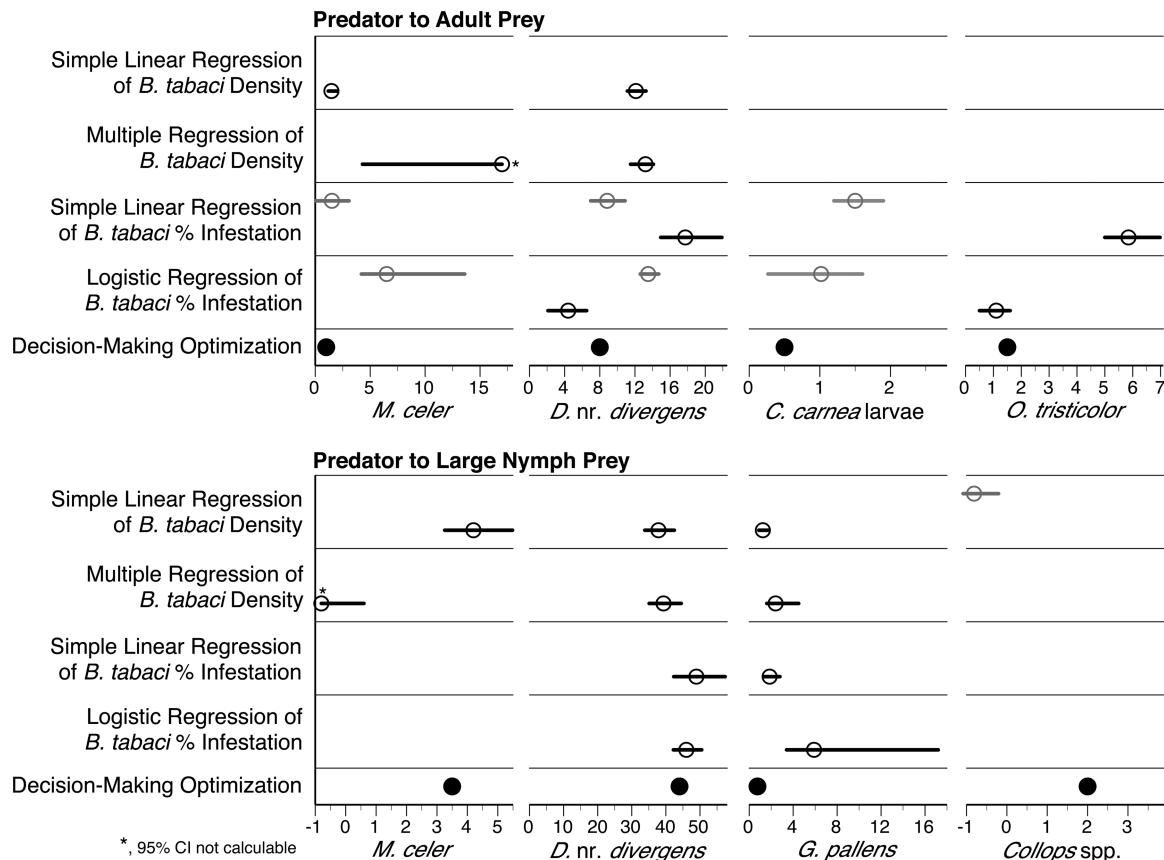




**Fig. 4.** Optimization for a range of ratios (x-axis) that encompass the estimated values identified via regression methods (see Fig. 5) for each of the key predator to *B. tabaci* ratios and the spray decision disagreement rates (y-axis) from 'early' and 'late' sprays using predator to *B. tabaci* ratios compared to the existing *B. tabaci* action threshold. Arrows show the refined biological control informed threshold recommended for pest managers.

*M. celer*, *D. nr. divergens*, *G. pallens*, *O. tristicolor*, *C. carnea*, and *Collops* spp. densities were significantly associated with declining pest densities. The former three were more consistently associated with prey densities in more than one analysis or year, suggesting them as more reliable measures of biological control of *B. tabaci* in this system. *M. celer* at 1 spider to 1 whitefly adult (per 100 sweeps and per leaf, respectively) or at 3.5 spiders per whitefly large nymph (per leaf disk), 8 *D. nr. divergens* per whitefly adult or 44 per whitefly large nymph, and 0.75 *G. pallens* per whitefly large nymph are each predator to prey ratios that mark critical levels

perithreshold for decision-making, or biological control informed thresholds. Predator to prey relationships falling below these critical levels when approaching the standard pest-centric threshold would be an indication of a biological control deficit, alerting the pest manager to advance chemical controls prior to the standard threshold. Conversely, predator to prey ratios exceeding these levels would indicate that biological control is operating at a level that should continue to suppress *B. tabaci* populations, even at or above the standard threshold. Under these conditions, the decision to spray could be deferred until the next sampling bout.



**Fig. 5.** Predator to *B. tabaci* ratios for *B. tabaci* adults and *B. tabaci* large nymphs ( $\pm 95\%$  CIs) for 2011 (open gray), 2012 (open black), and decision-making optimization for both years combined (solid black). Estimated ratios correspond to the *B. tabaci* action threshold and are estimated with either all significant predators (multiple regression and logistic regression) or no other effects (simple linear regressions) for both mean *B. tabaci* density (multiple regression analysis) or percent *B. tabaci* infestation (logistic regression analysis).

While these ratios were ultimately optimized independent of the presence of other predators and are each independent estimates of biological control predicted function, all predator interactions were examined in detail. Despite known antagonistic relationships like important intraguild predation that interferes with biological control (Rosenheim et al. 1993, 1999), we failed to find significant two-way or three-way interactions, positive or negative, among the generalist predators of this system that were associated with *B. tabaci* densities over both years of study. In just one case with nymphal infestation rates in 2012, *R. forticornis* or *Collops* spp. were positively associated with *B. tabaci* densities. Given that the cotton-*B. tabaci*, food web is large and complex (Naranjo and Ellsworth 2009b), it is perhaps not surprising that it is also flexible and compensatory to any shifting changes that might occur in prey or other resource availability in the system. This resilient capacity likely obscures momentary episodes of both positive and negative interactions among predators. While the generalist predators of this system can and do feed on one another (Hagler and Blackmer 2013), this behavior is likely opportunistic, especially when *B. tabaci* prey are relatively abundant. Predators also might be stimulated by other prey resources like honeydew (Hagen et al. 1971). High, but negative species weights in the PRC analyses for *C. carnea* suggested them to be lagging predators, precipitated by broad-spectrum insecticide use that released *B. tabaci* populations from control provided by other earlier responding predators. At this point, control of *B. tabaci* had likely already been lost but honeydew was abundant. Regardless of the mechanisms that may be operating subtly, there was a general

absence of predator interactions affecting outcomes relative to *B. tabaci* densities, further supporting the approaches taken to calculate independent estimates of ratios for each predator.

Given that independent, simple, and optimized analyses produced ratio estimates similar to those from more complex analyses (e.g., multiple regression inclusive of the presence and activity of multiple predators), the incorporation of these ratios into a pest management context is simplified. In general, this means more of each of these identified predators is helpful to the overall biological control of *B. tabaci*. When *B. tabaci* are at the standard threshold (three adults per leaf and one large nymph per disk), ratios would suggest that sprays would not be immediately needed if there were at least ca. 3–4 *M. celer*, 24–44 *D. nr. divergens*, 1–2 *Chrysoperla* larvae, 4–5 *O. tristicolor*, 1 *G. pallens*, and 2 *Collops* beetles per 100 sweeps. While each independently estimates a condition of favorable predator to prey dynamics, cumulatively this is more than 50 predators per 100 sweeps without even considering the presence of predators not associated with *B. tabaci* population declines. This represents a large amount of prey resource and food web flexibility in the system, though one must recognize that these dynamics will largely play out based on size with larger predators feeding on smaller ones in addition to *B. tabaci*.

Importantly, all of this work was performed in reference to a standard threshold that was itself developed in a context of naturally occurring biological control taking place in the background similar to other studies of biological control-based thresholds (Ostlie and Pedigo 1987, Walker et al. 2010, Giles et al. 2017). The standard threshold for *B. tabaci* was developed with the performance and

impact of selective chemistry carefully measured and described (Naranjo et al. 1998, Ellsworth et al. 2006, Naranjo and Ellsworth 2009b). Thus, these new ratios help quantify the potential contribution of biological control conserved through the usage of selective chemistries for control of *B. tabaci* and other target pests. These biological control informed thresholds are designed to identify whether natural enemies are present in sufficient abundance to indicate *B. tabaci* suppression perithreshold. They identify a target 'balance' of biological control at the *B. tabaci* action threshold, potentially reducing risk to pest managers by better classifying pest populations as damaging or benign and improving decision-making relative to the deployment of control tactics. Sufficient densities of predators might delay the need for insecticide sprays while insufficient densities may suggest the need to trigger earlier sprays to prevent economic damage. While these biological control informed thresholds are based on species-specific levels of conservation biological control, they probably operate more like proxies for the effects of the entire natural enemy community.

The general approach in this study was to establish varying predator to prey densities in manipulative field experiments subjected to different chemical exclusion regimes relative to untreated checks. Beyond the generalized limitations of any correlational study that prevents definitive statements of causation, this approach, as in most systems, was only able to effect reductions in predator or prey densities without any ability to augment populations. These results are therefore limited to the densities achieved; however, *B. tabaci* pressure varied greatly between the two field seasons. Even so, one regression relationship, *Collops* beetles to whitefly large nymphs, produced a predicted ratio that was negative. This was overcome through the decision optimization procedures that were still able to identify a local error minimum around two *Collops* to whitefly large nymphs. But, it calls into question the strength and reliability of this particular predator to prey relationship.

The decision optimization approach depends on the robustness of the previously established standard threshold, as it attempts to minimize decision errors relative to those levels. The *B. tabaci* two-stage thresholds are based in prevention of conditions that place the crop at risk for excess sugars or stickiness of fibers (Ellsworth et al. 1999, 2006), which itself is a relationship subject to large variation (Naranjo and Hequet 2007). Because the pest density to damage relationship is not based on yield, an easily measured parameter, but instead on predicted quality that has no field or experimental measurement system, there was no way to validate outcomes from the standard threshold, let alone these new biological control informed thresholds. This will be a limitation in future work to validate these thresholds.

However, the consistency of the results can be evaluated in two cases where predator ratios were identified for both whitefly prey life stages. With an adult threshold of three per leaf, the optimized ratio of *M. celer* to *B. tabaci* is 1 resulting in the need for 3 *M. celer* per 100 sweeps to defer a spray. For the large nymph threshold of one per disk, a condition defining population levels putatively equivalent to the adult threshold, 3.5 *M. celer* per 100 sweeps were needed to defer a spray. These predicted outcomes are in close agreement. Likewise, 24 or 44 *D. nr divergens* per 100 sweeps were needed to defer a spray for whitefly adults and large nymphs, respectively. These close agreements help to internally validate the approach used in this study to arrive at these ratios. Nevertheless, future work should be directed toward testing and validation of these individual thresholds and perhaps defining multiple predator indices or ratios that incorporate the weighted impact of numerous predators into a single threshold. A comparison to outcomes from control decisions made with the conventional *B. tabaci* action threshold will help to

identify the practical value of these new thresholds.

Arguably, the synthetic pyrethroids were the last group of truly broad-spectrum insecticides developed for agricultural use more than 40 yr ago (Elliott 1976). Many new modes of action have since been discovered, and we are now more than 20 yr into an era of greater availability of specific insecticides that have important qualities of narrow spectrum and selectivity toward beneficials. Yet, pest management science has lagged behind in the application of decision support systems that actively incorporate information about conserved biological control agents. In general, the development of thresholds informed by biological control have been rare (Hoffmann et al. 1990, Giles et al. 2003, Hamilton et al. 2004, Conway et al. 2006, Shakya et al. 2010, Walker et al. 2010, Hallett et al. 2014) with implementation even rarer (Naranjo et al. 2015, Giles et al. 2017). Many are based on parasitoid to prey relationships that are biologically and ecologically more tightly linked and therefore perhaps more tractable for research and implementation than generalist predator to prey relationships. Giles et al. (2017) outlined three barriers to adoption: demonstrating that 1) natural enemies can provide predictable pest suppression, 2) the basic elements of sampling and decision-making process can be easily integrated into current production systems, and 3) perhaps most importantly, growers see that the economic benefits outweigh the risks of adoption. Previous work in this system has amply demonstrated 'bioresidual' or the predictable pest suppression possible in cotton when selective insecticides are used (Naranjo and Ellsworth 2009a,b). Further, our proposed ratios build on arthropod sampling processes already used by growers and on-going validation research, analyses, and surveys suggest that they can be effectively used to reduce decision risk for economic benefit.

The Arizona cotton system has achieved broad-scale reductions in the usage of insecticides for the control of all arthropod pests, including the near elimination of use of broad-spectrum insecticides (Naranjo and Ellsworth 2009a; Ellsworth, unpublished data). In part, this supports the value that growers already place on biological control; cotton pest managers in Arizona estimated the value of conservation biological control at > \$100/ha (Naranjo et al. 2015). Biological control informed thresholds could help to enhance these positive changes while facilitating sustainability, arming growers with new ways to schedule the use of these selective insecticides. By identifying key predator to prey interactions that help maintain high yields and quality, these thresholds would permit the explicit incorporation of biological control into *B. tabaci* management, meeting pest management goals first presented over 50 yr ago (Stern et al. 1959) to integrate economic thresholds (for chemical controls) and biological control. By focusing on natural enemies in *B. tabaci* control decisions, we reinforce the value of selective insecticides while reducing perceived need for broad-spectrum chemistries. Such changes in pest management can reduce nontarget effects on beneficial organisms (e.g., natural enemies and pollinators), while reducing human health risk and facilitating improved economic outcomes.

## Supplementary Data

Supplementary data are available at *Journal of Economic Entomology* online.

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**Supplemental Table 1.** The relationship of ln-transformed predator to prey ratio to ln-transformed *B. tabaci* mean density in 2011 and 2012 shown in Figure 3.

Predator Taxon	<i>B. tabaci</i> Life Stage	Regression Type	Year	Relationship	df
<i>C. carnea</i>	Adult	Logistic	2011	$x = 0.6117 - 0.3088y$	1,43
<i>Collops</i> spp.	Large Nymph	Multiple	2011	$x = -0.6793 - 0.506y$	1,38
<i>D. nr. divergens</i>	Adult	Multiple	2012	$x = 4.976 - 1.5248y$	1,82
<i>D. nr. divergens</i>	Adult	Logistic	2011	$x = 0.9369 - 0.2379y$	1,43
<i>D. nr. divergens</i>	Adult	Logistic	2012	$x = 1.3101 - 0.3139y$	1,82
<i>D. nr. divergens</i>	Large Nymph	Multiple	2012	$x = 4.3503 - 1.2198y$	1,82
<i>D. nr. divergens</i>	Large Nymph	Logistic	2012	$x = 1.2602 - 0.2253y$	1,82
<i>G. pallens</i>	Large Nymph	Multiple	2012	$x = 1.0617 - 1.4071y$	1,82
<i>G. pallens</i>	Large Nymph	Logistic	2012	$x = 0.6473 - 0.2501y$	1,82
<i>M. celer</i>	Adult	Multiple	2012	$x = 2.9873 - 2.1315y$	1,82
<i>M. celer</i>	Adult	Logistic	2011	$x = 0.5465 - 0.1623y$	1,43
<i>M. celer</i>	Large Nymph	Multiple	2012	$x = 1.8122 - 1.1526y$	1,82
<i>O. tristicolor</i>	Adult	Logistic	2012	$x = 0.9691 - 0.3002y$	1,82

**Supplemental Table 2.** Proposed predator to *B. tabaci* ratios estimated from A), multiple regression analyses of *B. tabaci* density and B), logistic regression analyses of percent *B. tabaci* infestation. Inverse predictions incorporated all significant predator to prey ratios as explanatory variables for the appropriate *B. tabaci* life stage and year.

A.

Predator Taxon	<i>B. tabaci</i> lifestage	Year identified as significant	Predator to prey ratio estimation method		
			Simple linear regression	Inverse prediction	Decision-making optimization
<i>D. nr divergens</i>	Adult	2012	12.1 (11.1, 13.3) <sup>1</sup>	13.2 (11.5, 14.1)	8
<i>M. celer</i>	Adult	2012	1.5 (1.2, 1.9)	17 (4.3, •) <sup>2</sup>	1
<i>Collops</i> spp.	Large nymph	2011	-0.8 (-1.1, -0.2)	N/A <sup>3</sup>	2
<i>D. nr divergens</i>	Large nymph	2012	37.8 (33.8, 42.5)	39.3 (35.1, 44.5)	44
<i>G. pallens</i>	Large nymph	2012	1.2 (0.9, 1.7)	2.4 (1.6, 4.5)	0.75
<i>M. celer</i>	Large nymph	2012	4.2 (3.3, 5.5)	-0.8 (•, 0.6) <sup>2</sup>	3.5

B.

<i>C. carnea</i>	Adult	2011	1 (0.3, 1.6)	2 (1.6, 2.7)	0.5
<i>D. nr divergens</i>	Adult	2011	8.8 (7, 10.9)	13.5 (12.6, 14.7)	8
<i>D. nr divergens</i>	Adult	2012	17.7 (14.9, 21.9)	4.4 (2.1, 6.5)	8
<i>M. celer</i>	Adult	2011	1.5 (0.1, 3.1)	6.5 (4.2, 13.6)	1
<i>O. tristicolor</i>	Adult	2012	5.8 (5, 7)	1.1 (0.5, 1.6)	1.5
<i>D. nr divergens</i>	Large nymph	2012	48.9 (42.3, 57.4)	46 (42.2, 50.5)	44
<i>G. pallens</i>	Large nymph	2012	1.9 (1.3, 2.8)	5.9 (3.4, 17.2)	0.75

<sup>1</sup>Predator to prey ratios at the *B. tabaci* action threshold (lower, upper 95% confidence intervals)

<sup>2</sup>Not calculable

<sup>3</sup>The *Collops* spp. to large nymph ratio estimated by inverse predictions is equivalent to the ratio estimated by simple linear regression. Computationally, these produce negative threshold-intercept estimations of the ratios, however the decision-making optimization resulted in a positive ratio.