

Identification and Impact of Natural Enemies of *Bactericera cockerelli* (Hemiptera: Triozidae) in Southern California

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ABSTRACT *Bactericera cockerelli* (Sulc) (Hemiptera: Triozidae) is a major pest of potato, (*Solanum tuberosum* L.), tomato (*Solanum lycopersicum* L.), and peppers (*Capsicum* spp.). The purpose of our research was to identify and determine the impact of natural enemies on *B. cockerelli* population dynamics. Through 2 yr of field studies (2009–2010) at four different sites and laboratory feeding tests, we identified minute pirate bug, *Orius tristicolor* (White) (Hemiptera: Anthocoridae); western bigeyed bug, *Geocoris pallens* Stål (Hemiptera: Geocoridae), and convergent lady beetle, *Hippodamia convergens* Guérin-Ménéville (Coleoptera: Coccinellidae) as key natural enemies of *B. cockerelli* in southern California potatoes, tomatoes, and bell peppers. In natural enemy exclusion cage experiments in the potato crop and in American nightshade, *Solanum americanum* Miller, the number of *B. cockerelli* surviving was significantly greater in the closed cage treatments, thus confirming the affect natural enemies can have on *B. cockerelli*. We discuss how this information can be used in an integrated pest management program for *B. cockerelli*.

KEY WORDS Hemiptera, Coccinellidae, biological control, predator

The potato/tomato psyllid, *Bactericera cockerelli* (Sulc) (Hemiptera: Triozidae), is a serious pest of solanaceous crops such as potato (*Solanum tuberosum* L.), tomato (*Solanum lycopersicum* L.), peppers (*Capsicum* spp.), and eggplant (*Solanum melongena* L.) in Central and North America, and most recently in New Zealand (Cranshaw 1994, Liu and Trumble 2007, Teulon et al. 2009, Crosslin et al. 2010). This pest has caused millions of dollars in damage by direct feeding on crop plants and by transmitting a bacterial pathogen currently known as *Candidatus Liberibacter psyllae* (a.k.a. *Ca. L. solanacearum*) (Munyaneza et al. 2007, Hansen et al. 2008, Liefting et al. 2009, Crosslin et al. 2010).

One of the first assessments that should be made in an integrate pest management program is the potential role of natural enemies in controlling pests (Pedigo and Rice 2006). *B. cockerelli* is reportedly attacked by a number of natural enemies in North America (Cranshaw 1994). However, most of these reports are >40 yr old, focused on greenhouse populations, or they were published before the new invasive biotype moved into California (Liu and Trumble 2007).

In field locations in North America such as Arizona, New Mexico, Texas, and Utah, chrysopids, anthocorids, and coccinellids have been observed attacking *B. cockerelli* (Anonymous 1932, Knowlton 1933a, Romney 1939). Under artificial laboratory conditions, chrysopid larvae, coccinellids, geocorids, anthocorids,

mirids, nabids, and syrphid larvae have all been recorded to feed on *B. cockerelli* (Knowlton 1933a,b, 1934a; Knowlton and Allen 1936). A survey of potential predatory natural enemies of *B. cockerelli* in potatoes was conducted by Pletsch (1947) in potato fields and found geocorids, coccinellids, and chrysopids; although, no direct observations were made of these natural enemies attacking potato psyllid. Al-Jabr (1999) assessed two green lacewing species, *Chrysoperla carnea* Stephens and *Chrysoperla rufilabris* (Burmeister), as potential biological control agents of *B. cockerelli* in greenhouse tomato. These two chrysopid species could complete development on a diet of the *B. cockerelli*, but *C. rufilabris* was better adapted to surviving in the greenhouse environment (Al-Jabr 1999). A field trial involving augmentative additions of *C. carnea* to psyllid-infested potatoes did not result in the reduction of psyllid numbers (Al-Jabr 1999). Natural enemies of *B. cockerelli* also include two primary parasitoids: *Metaphycus psyllidis* Compere (Hymenoptera: Encyrtidae) and *Tamarixia triozae* (Burks) (Hymenoptera: Eulophidae). However, these two parasitoids have not provided significant control of *B. cockerelli* in bell pepper or potato crops (Compere 1943, Johnson 1971, Cranshaw 1994). Thus, throughout the years various studies have been conducted to document the natural enemies that attack *B. cockerelli*, but few studies have identified key natural enemies or their affect in the crop and noncrop habitats that this psyllid is known to inhabit (Romney 1939, Cranshaw 1994). The natural enemy community

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that attacks *B. cockerelli* is unknown in California. In addition, essentially no information on the potential population level suppression of natural enemies on *B. cockerelli* population dynamics is available (Goolsby et al. 2007).

At this time, within-field biological control has not been implemented, mostly because *B. cockerelli* are treated with pesticides even at extremely low infestation levels in an attempt to reduce pathogen transmission. Before biological control agents can be fully exploited in these systems, more studies are required to assess the effectiveness of predators and parasitoids on *B. cockerelli* populations in southern California. Thus, the objectives of this research were to identify key natural enemies of *B. cockerelli* in potato, tomato, and bell pepper plantings and to determine the impact of natural enemies on *B. cockerelli* in key crop and noncrop habitat in southern California. These data are a necessary first step in developing a regional management approach for this pest that includes natural enemies.

Materials and Methods

Surveys. Surveys were conducted throughout the 2009 and 2010 cropping seasons in potatoes, tomatoes, and bell peppers. Biweekly sampling surveys began 7 May 2009 and ended 3 December 2010. Commercial potato fields in Lakeview, CA (Riverside Co.) as well as tomato and bell pepper fields in Camarillo, CA (Ventura Co.) experienced pesticide applications. Organically grown bell pepper plants were also surveyed in Oxnard, CA (Ventura Co.) in 2009. Insecticide-free potato, tomato, and bell pepper plantings were sampled at the University of California, South Coast Research and Extension Center in Irvine, CA (Orange Co.). Thus, we covered a wide range of production systems and practices to find potential natural enemies.

Collection techniques included visual counts (both destructive sampling and in situ counts of potential natural enemies on the crop plants) and sweep netting of arthropods within agricultural fields. For the commercial fields, visual counts were conducted using a systematic sampling design whereby a total of 15–25 plants per field per sample date were examined. These plants were sampled from three to five transects within a field at every 20 m for up to 80 m on each sample date. In addition, a 38-cm diameter sweep net was used for sampling arthropods in the crop foliage by using a prearranged M-shaped pattern with 25 sweeps per sampling point within the field. At the Orange Co. crop plantings, 8–15 plants were examined randomly within four plots per sampling date, and an additional 20 sweeps per plot were collected. The number of natural enemies and the number of *B. cockerelli* that occurred on infested plants also were recorded.

Other alternative prey species were present and recorded from all fields, and included aphids, thrips, whiteflies, flea beetles, lepidopteran caterpillars, mirids, and *Lygus hesperus* (Knight); however, *B. cockerelli*

was the most abundant insect in all fields examined. Voucher specimens of potential natural enemies were deposited at the Entomology Research Museum, University of California, Riverside.

Laboratory Feeding Assays. Results from the surveys indicated that some natural enemy species were more abundant than others. Based on the results of the relative abundance to natural enemies from the surveys, six natural enemies were further tested in laboratory feeding assays. *B. cockerelli* were reared and maintained according to the methods described by Butler et al. (2011). Predators were collected from bell peppers 31 August–28 September 2010 from Irvine, CA. Predators were added to a 9-cm-diameter petri dish that contained a moistened filter paper and an excised tomato leaf with 20 eggs, 20 second–third instar nymphs, and 10 adult *B. cockerelli* ($n = 7$ –20 petri dish arenas per predator species depending on availability, and 29 control replicates with no predators to account for nonpredator mortality). Predators had access to *B. cockerelli* for a 24-h period. At the end of the 24-h period, the numbers of *B. cockerelli* attacked in all life stages were counted, and the percentage of mortality was calculated per stage.

Exclusion Cage Studies. These experiments were conducted in late-season plantings of potato and the American nightshade, *Solanum americanum* Miller, in 2009 and 2010 at the University of California South Coast Research and Extension Center in Orange Co. *B. cockerelli* has a wide host range and this psyllid is able to oviposit and complete development on >40 host species (Knowlton and Thomas 1934) but is most commonly found on solanaceous plants (Al-Jabr 1999). Experimental plots were established using a 2 by 2 factorial design. The first factor involved type of plant: potatoes or American nightshade. Nightshade plots were established 1 m distant from the potato plots to minimize potential environmental variability. The second factor varied exposure of *B. cockerelli* to natural enemies by using exclusion cages. Cage treatments were either closed, open (frame structure without screen) or no cages (after Van Driesche et al. 2008). A 7.0- by 7.5-cm cage with thrips-proof mesh (SpiderNet+, Meteor Agricultural Nets Ltd., Israel) was placed over the terminal leaflet on the upper third of the plant.

Leaflets were cleared of psyllids and natural enemies before 10–15 lab-reared first–second instar nymphs were added to each leaflet and allowed to settle for 24 h. Preliminary observations showed that *B. cockerelli* nymphs are sedentary and would remain on the leaves (C.D.B., unpublished data). After 24 h, the number of psyllids remaining was confirmed and then the appropriate cage treatment was added. Cages were checked every 2–4 d until psyllids were no longer found. These experiments were conducted as a randomized complete block design with three blocks in 2009 and four blocks in 2010. Each block consisted of one replicate of the plot treatments, with two replicates of each cage treatment.

Data Analysis. Multiple linear regressions were used to analyze the number of natural enemies that occur

on *B. cockerelli*-infested crop plants. Because of significant interactions ($P < 0.05$) between the number of *B. cockerelli* that occur on crops by year and location (except for potatoes), we examined the regressions for each year and locality on each crop individually. Because of pesticide applications in the commercial fields, regression analyses also were conducted individually so a comparison could be made between the commercial and insecticide-free plots.

The average number of *B. cockerelli* that occurred on crop plants were first analyzed by using analysis of variance (ANOVA) in a general linear models procedure of SAS version 9.2 (PROC GLM, SAS Institute 2008). The mean numbers of psyllids per crop plant were log transformed, reciprocal square root transformed, and reciprocally transformed to homogenize variances and normalize the data for bell pepper, tomatoes, and potatoes, respectively. When there was a significant interaction ($P < 0.05$) between year and location, multiple comparison tests using the LSMEANS/PDIFF option with a Tukey adjustment were done to discriminate differences among the means. After the transformation of the dependent variable, stepwise selection criteria were used to find the natural enemies that best described the relationship for the number of psyllids on the crop plants. Confirmation of the best model was tested using adjusted R^2 , Akaike Information Criterion (AIC), Bayesian Information Criterion (BIC), and Mallows' C_p criteria. In general, all model ranking tests agreed on which model was the best after the stepwise selection criteria. Thus the model seems robust. The merits of individual model rating statistics can be found in Burnham and Anderson (2002).

Multiple regressions alone can be difficult to interpret; a high density of pests other than just psyllids could attract natural enemies (particularly generalists) and lead to a positive correlation that is statistically significant yet not primarily due to a response to psyllids. To determine whether the relationships seen for the multiple regression data were confounded by this or related problems, we graphed the total natural enemies versus the psyllid populations (Fig. 1). To avoid potential conflicts with pesticide selection and use, data are presented for pesticide-free tomato, potato, and pepper fields sampled in 2009 and 2010. Values are total numbers of psyllids and natural enemies found on any given date.

For the laboratory feeding assays, the numbers of *B. cockerelli* in all life stages attacked within the 24-h exposure with the potential predator were compared with controls and against each other using a general linear model (PROC GLM, SAS Institute 2008). When a treatment factor was significant ($P < 0.05$), a probability difference with a Tukey adjustment was used to discriminate difference among the treatment means.

For the exclusion cage studies, the numbers of psyllids per cage were first tested between the open and uncaged treatments to rule out possible cage effects (Van Driesche et al. 2008). The mean numbers of psyllids in the open and uncaged treatments were tested by year using ANOVA in general linear models

procedure of SAS. Both a repeated measures and mixed linear effects models were tested. Results were essentially the same, but the repeated measures model produced biologically questionable interactions that were contradictory. We therefore report the results from the general linear models procedure. Analysis of these data revealed no significant ($P > 0.05$) cage effects so data from uncaged and open treatments were pooled. The numbers of psyllids per cage treatment were square root transformed to homogenize variances and normalize the data. Exclusion cage data were then analyzed using ANOVA in a general linear models procedure of SAS. When there was a significant interaction ($P < 0.05$) between year, date, plot and cage type, multiple comparison tests using the LSMEANS/PDIFF option with a Tukey adjustment were done to discriminate differences among the means.

Results

Surveys. A variety of natural enemies were recorded during the 2-yr study for each of the solanaceous crops examined (Table 1). In total, 15 different spider genera in nine families were represented in this survey. Potential insect predators included 23 genera from 15 families. The most abundant groups included coccinellids as well as three species of Hemiptera. From the species of coccinellids identified, convergent lady beetle, *Hippodamia convergens* Guérin-Ménéville, made up the majority consisting of 59.5% of the samples. Two other coccinellids made up >5% of the samples included sevenspotted lady beetle, *Coccinella septempunctata* L. (24.3%), and multicolored Asian lady beetle, *Harmonia axyridis* (Pallas) (8.1%). Minute pirate bug, *Orius tristicolor* (White) and *Geocoris pallens* Stål were present in all fields examined. The mirid *Cyrtopeltis modesta* (Distant) was very abundant in Orange Co. tomatoes (2009 and 2010) and potatoes (2010). Eggs from *Chrysoperla* spp. were present in all fields as well; however, larvae and adults were much less common and not found in all fields. Parasitoids reared from potato psyllids included *T. triozae* and *M. psyllidis*. *T. triozae* was present in all of the fields with the exception of potatoes in 2009; however, the percentage of parasitism was <20%. *M. psyllidis* was rare (<2% of the parasitoids reared out of *B. cockerelli*) and only occurred in bell peppers in 2009.

Multiple Regression Analyses. The mean number of *B. cockerelli* per plant by year and location are listed in Table 2. For bell peppers, there was a significant interaction between year and county for the number of *B. cockerelli* per plant ($F = 20.31$; $df = 1, 279$; $P < 0.0001$). For bell peppers, the natural enemies such as spiders, coccinellids, *G. pallens*, *O. tristicolor*, and the parasitoid *T. triozae* exhibited significant relationships between the numbers of these natural enemies on plants that were infested with *B. cockerelli* (Table 2).

For bell peppers in Orange Co. in 2009, the overall model was significant ($F = 7.64$; $df = 2, 32$; $P = 0.0019$) and included spiders ($\beta = -0.55$; $F = 7.57$; $df = 1, 32$; $P = 0.0097$) and coccinellids ($\beta = 0.56$; $F = 4.77$; $df =$

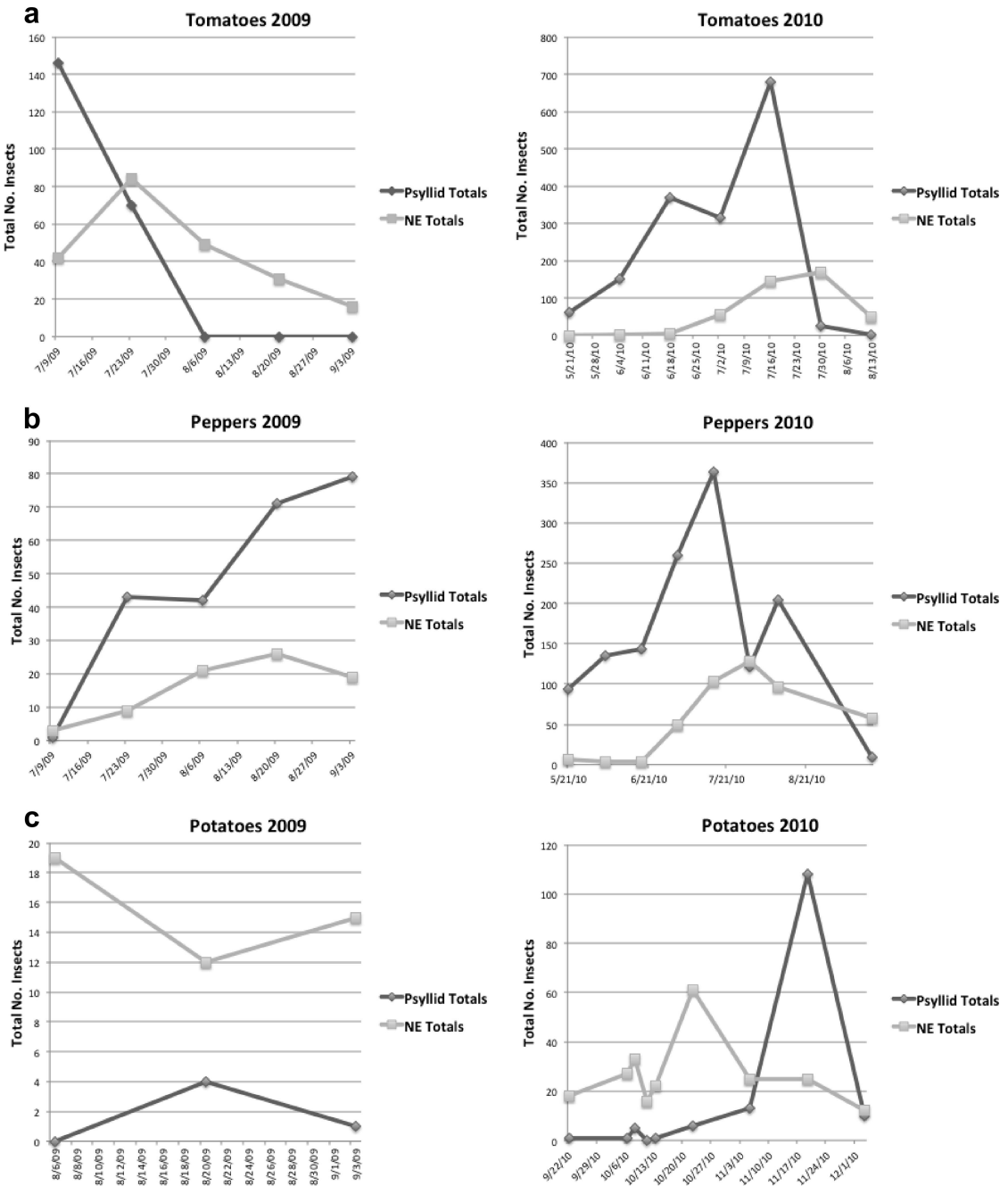


Fig. 1. Relationships between total numbers of natural enemies and psyllids over time in 2009 and 2010 plantings of tomatoes (a), bell peppers (b), and potatoes (c) that were not exposed to pesticides.

1, 32; $P = 0.0363$) as natural enemies that described the mean number of psyllids per plant ($R^2 = 0.32$). There were on average 0.51 ± 0.12 spiders and 0.14 ± 0.09 coccinellids per plant infested by potato psyllids. In Ventura Co. bell peppers in 2009, the overall model was significant ($F = 7.98$; $df = 1, 80$; $P = 0.0060$) and only included *G. pallens* ($\beta = -0.84$; $F = 7.98$; $df = 1, 80$; $P = 0.0060$) as a natural enemy that described the

relationship for the number of *B. cockerelli* per plant ($R^2 = 0.09$). The mean number of *G. pallens* per psyllid-infested plants was 0.13 ± 0.05 .

In 2010 for Orange Co. bell peppers, both *G. pallens* ($\beta = 0.90$; $F = 8.37$; $df = 1, 73$; $P = 0.0050$) and *O. tricolor* ($\beta = 0.44$; $F = 4.31$; $df = 1, 73$; $P = 0.0415$) were included in the overall significant model ($F = 8.76$; $df = 2, 73$; $P = 0.0004$) ($R^2 = 0.19$), and in Ventura

Table 1. Continued

Order/family	Species	2010										Total						
		2009					2010											
		Bell pepper		Potato		Tomato		Bell pepper		Potato			Tomato					
Orange Co.	Ventura Co.	Orange Co.	Riverside Co.	Orange Co.	Ventura Co.	Orange Co.	Ventura Co.	Orange Co.	Ventura Co.	Orange Co.	Ventura Co.	Orange Co.	Ventura Co.					
Hymenoptera																		
Eucyrtidae	<i>M. psyllidis</i>	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5
Eulophidae	<i>T. triozae</i>	10	4	-	-	8	35	8	19	11	1	1	5	175	5	1	1	273
Formicidae	<i>Lanopthema humile</i>	8	1	5	-	3	1	3	8	-	12	-	-	-	-	-	-	39
Hemiptera																		
Anthocoridae	<i>O. tristicolor</i>	1	43	3	2	86	26	41	49	41	13	7	55	11	337	-	-	337
Berytidae	<i>Pronolaccanthis annulata</i>	-	-	-	1	-	-	-	1	-	-	1	-	-	5	-	-	5
Geocoridae	<i>G. pallens</i>	2	19	2	36	1	3	1	24	6	1	9	36	17	156	-	-	156
Miridae	<i>C. modesta</i>	-	17	2	11	108	37	5	7	5	144	1	200	13	545	-	-	545
Nabidae	<i>Nabis</i> spp.	-	-	-	3	2	-	-	10	-	1	3	-	-	19	-	-	19
Reduviidae	<i>Empicoris</i> spp.	-	1	-	1	-	-	-	-	-	-	-	-	-	2	-	-	2
Neuroptera																		
Chrysopidae	<i>Chrysoperla</i> spp. eggs	16	15	25	38	4	26	4	76	85	24	53	24	9	395	-	-	395
	<i>Chrysoperla</i> spp. larvae	1	1	1	6	1	1	1	-	3	1	-	-	1	15	-	-	15
	<i>Chrysoperla</i> spp. adults	-	-	-	3	1	-	1	5	-	1	-	1	-	12	-	-	12
Hemeroptera	Unidentified adult	-	-	-	-	-	-	-	-	1	-	-	-	-	1	-	-	1
Total		69	115	62	176	294	137	294	357	191	302	137	489	245	2,574	-	-	2,574

Co. *O. tristicolor* ($\beta = -0.43$; $F = 6.25$; $df = 1, 87$; $P = 0.0143$) and parasitism by *T. triozae* ($\beta = 0.10$; $F = 10.22$; $df = 1, 87$; $P = 0.0019$) were included in the overall significant model ($F = 8.92$; $df = 2, 87$; $P = 0.0003$) that described the relationship between the number of psyllids per bell pepper plant ($R^2 = 0.17$). On *B. cockerelli*-infested plants in 2010, there was an average of 0.28 ± 0.08 *G. pallens* and 0.45 ± 0.12 *O. tristicolor* per plant in Orange Co. and 0.31 ± 0.08 *O. tristicolor* and 1.21 ± 0.43 *T. triozae*-parasitized psyllids per plant in Ventura Co.

There was a significant interaction between year and county for the mean number of *B. cockerelli* that occurred on tomatoes ($F = 23.65$; $df = 1, 261$; $P < 0.0001$). Natural enemies in tomatoes that exhibited significant relationships with the number of *B. cockerelli* per plant included spiders, *G. pallens*, *O. tristicolor*, and *T. triozae* (Table 2). For tomatoes in Orange Co. in 2009, the overall model was significant ($F = 7.38$; $df = 1, 57$; $P = 0.0087$) and only included *O. tristicolor* ($\beta = -0.05$; $F = 7.38$; $df = 1, 57$; $P = 0.0087$) as a natural enemy that described the relationship for the number of *B. cockerelli* per plant ($R^2 = 0.11$). The mean number of *O. tristicolor* per tomato plant was 1.34 ± 0.27 .

In Ventura Co. tomatoes in 2009, overall model was significant ($F = 6.52$; $df = 3, 69$; $P = 0.0005$) and included spiders ($\beta = -2.15$; $F = 6.03$; $df = 1, 69$; $P = 0.0165$), *G. pallens* ($\beta = -3.02$; $F = 4.83$; $df = 1, 69$; $P = 0.0313$), and *T. triozae* ($\beta = 0.03$; $F = 5.93$; $df = 1, 69$; $P = 0.0175$) as natural enemies that described the mean number of psyllids per plant ($R^2 = 0.23$). There was an average of 0.11 ± 0.04 , 0.04 ± 0.02 , and 5.58 ± 2.82 spiders, *G. pallens*, and *T. triozae*-parasitized psyllids per tomato plant that contained psyllids, respectively. For tomatoes in Orange Co. in 2010, the overall model was significant ($F = 6.48$; $df = 1, 72$; $P = 0.0131$) and only included *G. pallens* ($\beta = -0.36$; $F = 6.48$; $df = 1, 72$; $P = 0.0131$) as a natural enemy that described the relationship for the number of *B. cockerelli* per plant ($R^2 = 0.08$). The mean number of *G. pallens* per *B. cockerelli*-infested plants was 0.49 ± 0.15 .

In Ventura Co. tomatoes in 2010, *G. pallens* ($\beta = -2.28$; $F = 22.31$; $df = 2, 56$; $P < 0.0001$) and parasitism by *T. triozae* ($\beta = 0.03$; $F = 16.12$; $df = 2, 56$; $P = 0.0002$) were included in the overall significant model ($F = 23.04$; $df = 2, 56$; $P < 0.0001$) to describe the relationship between the numbers of psyllids per plant ($R^2 = 0.45$). There was an average of 0.29 ± 0.07 *G. pallens* and 9.58 ± 4.14 *T. triozae*-parasitized psyllids per *B. cockerelli*-infested plant.

For potatoes, there was no significant effect of year ($F = 0.03$; $df = 1, 181$; $P = 0.8562$) and county ($F = 2.08$; $df = 1, 181$; $P = 0.1507$) regarding the number of *B. cockerelli* per plant nor was the interaction between year and county significant ($F = 1.85$; $df = 1, 181$; $P = 0.1749$) (Table 2). There were no significant relationships for the number of *B. cockerelli* per potato plant for Orange Co. in 2009 or Riverside Co. in 2009 and 2010. Only for potatoes in Orange Co. in 2010, the overall model was significant ($F = 10.79$; $df = 2, 59$; $P = 0.0001$) and included *O. tristicolor* ($\beta = -0.19$; $F = 4.40$; $df = 1, 59$; $P = 0.0403$) and parasitism by *T. triozae*

Table 2. Multiple regression analyses to describe the relationship between the number of *B. cockerelli* and the number of natural enemies per plant

Crop	Multiple regression results by year and location							
	2009, Orange Co.		2009, Ventura Co.		2010, Orange Co.		2010, Ventura Co.	
Bell pepper								
Psyllids per plant								
Intercept	6.7 ± 1.3a	14.9 ± 2.1ab	17.5 ± 2.0b	154.6 ± 23.3c				
Araneae spp.	1.83 ± 0.18	Parameter estimate (± SE) 2.27 ± 0.13	Parameter estimate (± SE) 3.37 ± 0.23	Parameter estimate (± SE) 4.27 ± 0.14				
Coccinellids	-0.35 ± 0.20							
<i>C. pallens</i>	0.56 ± 0.25							
<i>O. tristicolor</i>		-0.84 ± 0.30	0.0060	0.0050				
<i>T. tritoxae</i>				0.0415				
F	7.64	7.98	8.76	8.92				
df	2, 32	1, 80	2, 73	2, 87				
P > F	0.0019	0.0060	0.0004	0.0003				
R ²	0.3233	0.0907	0.1935	0.1702				
	2009, Orange Co.	2009, Ventura Co.	2010, Orange Co.	2010, Ventura Co.				
Tomato								
Psyllids per plant								
Intercept	3.7 ± 1.5a	457.6 ± 212.8c	21.7 ± 5.1b	201.1 ± 58.5bc				
<i>O. tristicolor</i>	0.93 ± 0.04	3.74 ± 0.30	2.01 ± 0.20	3.40 ± 0.30				
<i>C. pallens</i>	-0.05 ± 0.02							
Araneae spp.		-3.02 ± 1.38	-0.36 ± 0.14	-2.28 ± 0.48				
<i>T. tritoxae</i>		-2.15 ± 0.88						
F	7.38	6.72	6.48	6.48				
df	1, 57	3, 69	1, 72	2, 56				
P > F	0.0087	0.0005	0.0131	<0.0001				
R ²	0.1146	0.2261	0.0826	0.4514				
	2009, Orange Co.	2009, Riverside Co.	2010, Orange Co.	2010, Riverside Co.				
Potato								
Psyllids per plant								
Intercept	0.33 ± 0.13a	3.84 ± 1.0a	2.3 ± 1.0a	2.8 ± 0.9a				
<i>O. tristicolor</i>			0.83 ± 0.04					
<i>T. tritoxae</i>			-0.19 ± 0.09					
F			-0.56 ± 0.16					
df			10, 79					
P > F			2, 59					
R ²			0.0001					
			0.2678					

Table 3. Number (mean \pm SE) of *B. cockerelli* attacked and percentage mortality in 24-h no-choice feeding trials with potential predators from bell pepper, 31 August–28 September 2010, Irvine, CA

Order/family	Species	n	<i>B. cockerelli</i> adults		<i>B. cockerelli</i> nymphs		<i>B. cockerelli</i> eggs	
			No. attacked ^a	% mortality	No. attacked ^a	% mortality	No. attacked ^a	% mortality
Coleoptera								
Coccinellidae	<i>C. septempunctata</i>	7	5.3 \pm 1.2bc	53	9.1 \pm 2.2bc	39	0.0 \pm 0.0a	0
	<i>H. axyridis</i>	18	8.5 \pm 0.6a	85	17.2 \pm 1.7a	72	2.7 \pm 0.8ab	12
	<i>H. convergens</i>	20	7.1 \pm 0.7ab	71	15.5 \pm 0.9a	77	6.5 \pm 1.5b	32
Hemiptera								
Anthocoridae	<i>O. tricolor</i>	20	1.8 \pm 0.3e	18	9.7 \pm 1.1c	48	3.0 \pm 1.0a	14
Miridae	<i>C. modesta</i>	20	0.8 \pm 0.2de	8	6.2 \pm 0.8bc	31	0.8 \pm 0.4ab	4
Neuroptera								
Chrysopidae	<i>Chrysopa</i> spp. larvae	17	2.9 \pm 0.5cd	28	14.4 \pm 1.0ab	66	6.6 \pm 1.5b	27
Control		29	1.2 \pm 0.2e	12	1.7 \pm 0.4d	9	0.6 \pm 0.2a	3

^a Means within a column for the respective *B. cockerelli* life stage followed by different letters are significantly different using PROC GLM of SAS.

($\beta = -0.56$; $F = 12.57$; $df = 1, 59$; $P = 0.0008$), which described the mean number of *B. cockerelli* per plant ($R^2 = 0.27$). There was an average of 0.13 ± 0.05 *O. tricolor* and 0.06 ± 0.03 *T. triozae*-parasitized *B. cockerelli* per potato plant that contained psyllids.

The relationships between total natural enemies and psyllid populations were informative (Fig. 1). In tomato plantings (Fig. 1a), populations of psyllids declined following a peak in early July of 2009 and mid-July in 2010 as natural enemy densities increased. Natural enemy populations peaked 2–3 wk later in both years, supporting the relationships calculated with the multiple regression analyses. For bell peppers (Fig. 1b), numbers were fairly low in 2009 and the natural enemies were not efficient at controlling the psyllids. In contrast, the much higher values seen in 2010 again provided a bimodal distribution. The population of psyllids peaked in mid-July followed by a rapid decline as the density of beneficials increased (peak of beneficials was 30 July 2010). There were no clear patterns seen with psyllid and natural enemy populations in potatoes (Fig. 1c), also supporting the results seen with the multiple regression analyses.

Laboratory Feeding Assays. From this list of potential *B. cockerelli* predators, a subset of natural enemies was tested in laboratory trials to determine whether they could consume potato psyllids and which stages they could attack (Table 3). All of the predators except *C. modesta* and *O. tricolor* attacked significant numbers of adults compared with the control ($F = 40.62$; $df = 6, 124$; $P < 0.0001$). *H. axyridis* attacked the most adults in 24 h compared with all other predators with the exception of *H. convergens*, and the percentage of mortality inflicted upon *B. cockerelli* adults was greatest for *H. axyridis* at 85%. Likewise, *Chrysoperla* spp. larvae also could successfully attack significant number of adults.

For the immature stages of the potato psyllids, all of the natural enemies tested attacked significant numbers of *B. cockerelli* nymphs ($F = 42.94$; $df = 6, 124$; $P < 0.0001$). Only *H. convergens* and *Chrysoperla* spp. larvae were able to attack significant numbers of *B. cockerelli* eggs ($F = 6.11$; $df = 6, 124$; $P < 0.0001$).

Exclusion Cage Study. There were significant differences in the number of *B. cockerelli* nymphs that

survived by year ($F = 126.26$; $df = 1, 307$; $P < 0.0001$), date ($F = 264.64$; $df = 3, 307$; $P < 0.0001$), habitat (i.e., potato versus nightshade) ($F = 4.41$; $df = 1, 307$; $P = 0.0366$), and cage type ($F = 187.37$; $df = 1, 307$; $P < 0.0001$). Based on these results, the numbers of psyllids that survived per cage type were analyzed separately in the potato crop and nightshade plots by year and date (Figs. 2 and 3). Within the potato crop, the average number of *B. cockerelli* that survived was significantly greater in the closed cages compared with the open cages ($F = 55.40$; $df = 1, 145$; $P < 0.0001$). Similar dynamics occurred within the nightshade plots. Significantly more psyllids survived in the closed cages versus the open cages ($F = 143.36$; $df = 1, 145$; $P < 0.0001$). Natural enemies observed in the plots during the time of these experiments included spiders, *H. convergens*, *C. septempunctata*, *H. axyridis*, *O. tricolor*, *G. pallens*, *Nabis* spp., *C. modesta*, *Chrysoperla* spp. larvae, and syrphid larvae.

Discussion

Based on the data from the surveys, regression analyses, and laboratory feeding assays, we have identified *O. tricolor*, *G. pallens*, and *H. convergens* as key natural enemies of *B. cockerelli* in southern California, which may warrant further research for natural enemy conservation or augmentation in the crop and non-crop habitats. The numbers of *O. tricolor* exhibited significant relationships with the number of *B. cockerelli* per plant in bell peppers in Orange and Ventura Cos. in 2010, tomatoes in Orange Co. in 2009, and potatoes in Orange Co. in 2010. Furthermore, *O. tricolor* was observed attacking *B. cockerelli* in bell peppers in Ventura Co., 2010 (our unpublished data). As with the observations by Knowlton and Allen (1936), our results corroborate that *O. tricolor* is a predator of *B. cockerelli* but go beyond their observations to show that this predator is able to attack significant numbers of nymphs and adults. For the predator *G. pallens*, previous work by Pletsch (1947) in Montana only found this predator in potatoes, whereas Knowlton (1934a) noted *Geocoris decoratus* Uhler in potatoes in Utah and tested this species in the laboratory

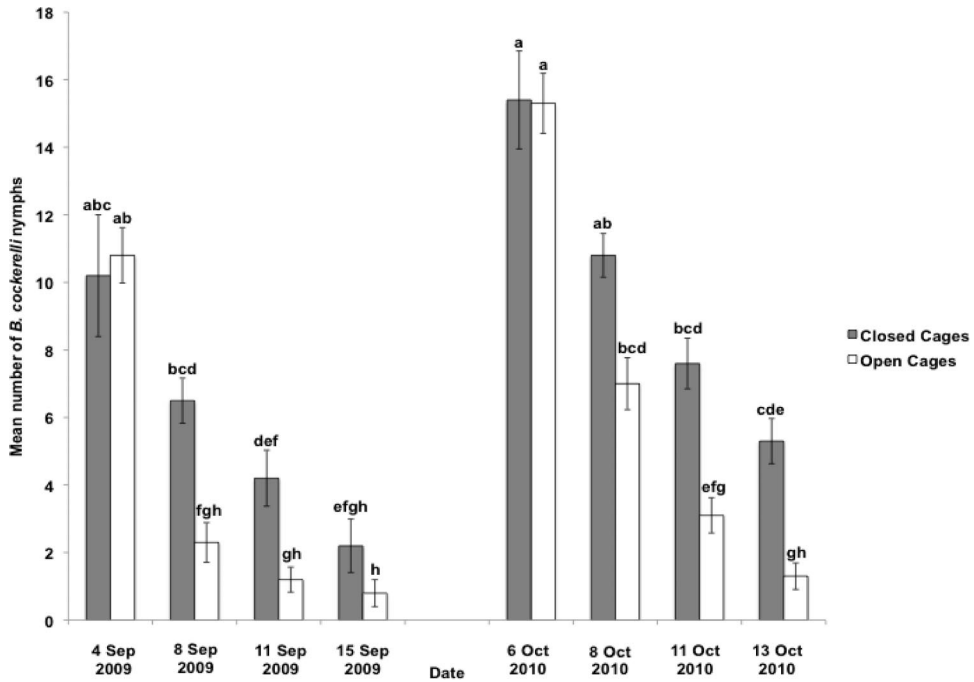


Fig. 2. Number (mean \pm SE) of potato psyllids per cage type by year and date in potatoes plots at the University of California South Coast Research and Extension Center, Orange Co., CA ($F = 32.95$; $df = 21,145$; $P < 0.0001$). Bars associated with different letters are significantly different using the LSMEANS/PDIFF option with a Tukey adjustment.

as a predator of *B. cockerelli*. Our research has shown that *G. pallens* exhibits significant relationships with *B. cockerelli* in bell peppers in Ventura Co. in 2009 and Orange Co. in 2010, and tomatoes in Ventura Co. in 2009–2010 and in Orange Co. in 2010. Like *O. tristicolor*, this predator was present in all fields examined and lends support to this predator being a natural enemy of *B. cockerelli*.

Only coccinellids exhibited significant relationships with the number of psyllids per pepper plant in Orange Co. in 2009. Again *H. convergens* accounted for 59.5% of the coccinellids found. This is similar to the observations made in surveys conducted >60 yr ago by Pletsch (1947). *H. convergens* also consumed significant numbers of all life stages of *B. cockerelli*. However, in direct observations in the field we have observed *H. convergens* ignoring *B. cockerelli* eggs while searching for prey (our unpublished data). Thus, further tests may be needed to verify the importance of egg predation on psyllid mortality. Additional tests may be justified because egg feeding by the coccinellid *Diomus pumilio* (Weise) has been reported as an important contributing factor in suppression of another psyllid, *Acizzia uncatoides* (Ferris & Klyver) (Pinnock et al. 1978). Romney (1939) also reported that coccinellids (unidentified species) can reduce the number of eggs and nymphs of *B. cockerelli* in *Lycium* spp. in southern Arizona, New Mexico, and Texas.

Numerous spider species were observed and present in all fields examined. Spiders in bell peppers in Orange Co. in 2009 and in tomatoes in Ventura Co. in 2009 exhibited significant relationships with the num-

ber of *B. cockerelli* per plant. Further experiments may be needed to determine which species may be most important, but in direct observation in bell peppers in Orange Co. the species *Cyclosa turbinata* Walckanaer (Araneae: Araneidae) produced webs that had trapped *B. cockerelli* adults (our unpublished data).

Although the parasitoid *T. triozae* has not provided significant control of *B. cockerelli* in previous experiments (Johnson 1971), we believe there is potential for this parasitoid to be used as a control agent in noncrop habitats or crops that are not repeatedly treated with pesticides. Parasitoids in the genus *Tamarixia* have been used successfully as biocontrol agents against other psyllid species (Dahlsten et al. 1995, Kennett et al. 1999). The number of parasitized *B. cockerelli* exhibited significant relationships in many of the crops we surveyed in southern California; however, despite this, the percentage of parasitism in agricultural fields was low (<20%). In particular, the multiple regression analyses for total natural enemies and the graphs in Fig. 1 show that where the psyllid specialist *T. triozae* accounted for ≈ 40 –55% of the total natural enemy density (bell peppers and tomatoes, respectively), the relationships indicated potentially useful biological control. Similarly, Romney (1939) made the claim that *T. triozae* could reduce the number of nymphs of *B. cockerelli* in *Lycium* spp., but details were sparse. In our samples from potatoes, where more than two thirds of the natural enemies were generalists, the lack of relationships in either the multiple regression analyses or the graphical data (Fig. 1c) suggested that the

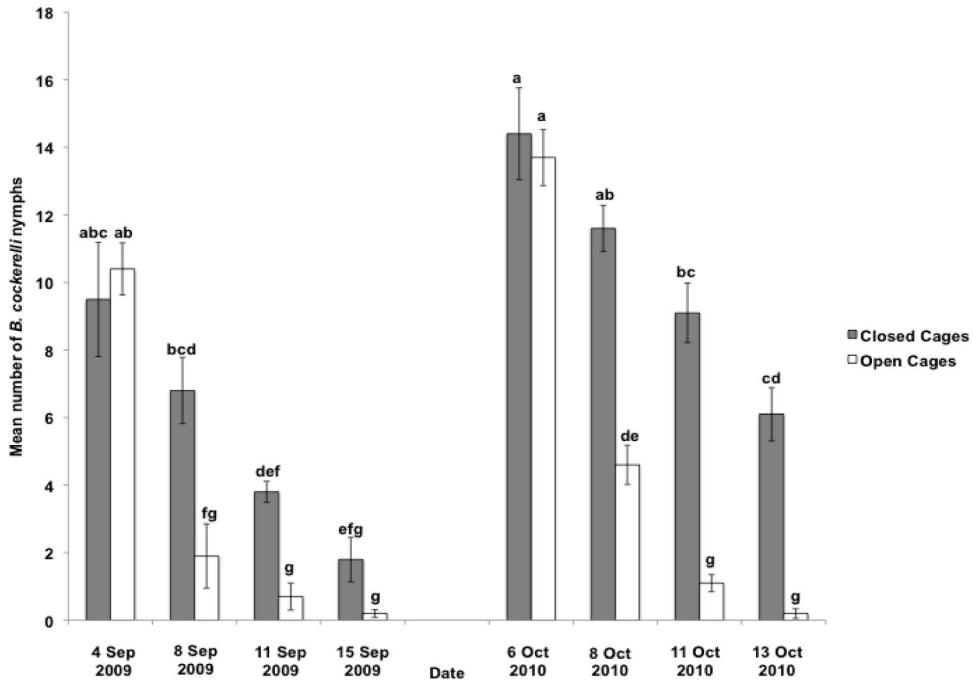


Fig. 3. Number (mean \pm SE) of potato psyllids per cage type by year and date in nightshade plots at the University of California South Coast Research and Extension Center, Orange Co., CA ($F = 47.57$; $df = 21, 145$; $P < 0.0001$). Bars associated with different letters are significantly different using the LSMEANS/PDIFF option with a Tukey adjustment.

complex of natural enemies as a whole were not responding specifically to the psyllids.

Some caution should be noted with these results as many of the natural enemies that exhibited significant relationships with the number of psyllids per plant, the range of R^2 values (0.08–0.45, Table 2) suggest that the natural enemies may not show a predictive relationship with *B. cockerelli* in agricultural fields. Plants with high numbers of predators may attract or arrest more natural enemies than plants with low numbers, leading to a correlation. In contrast, efficient natural enemies might subsequently lower the pest densities, resulting in a negative correlation. However, our primary goal was to identify potential candidates for biological control, so we focused on determining which natural control agents were present and if there was a statistical relationship between psyllids and natural enemies over the course of the crop cycles. For example, although other potential predators tested in the laboratory included *Chrysoperla* spp. larvae and *C. modesta*, which attacked significant number of *B. cockerelli* nymphs, the number of these predators did not correlate with the number of *B. cockerelli* that occurred on crop plants. Numerous *Chrysoperla* spp. eggs were found in the field, but very few *Chrysoperla* spp. larvae, suggesting that larval *Chrysoperla* spp. may experience heavy intraguild predation (Rosenheim et al. 1999).

No studies to date have systematically examined the effects of natural enemies on *B. cockerelli* in crops, much less on noncultivated host plants. Thus, we currently have minimal information on the role that natural enemies might be playing in suppression of the

psyllid populations. Our data from the exclusion cage study is the first to suggest that natural enemies can have an impact on the survival of *B. cockerelli* in a field crop or a noncrop host plant. Just 2 d after initiation of the experiment, the number of *B. cockerelli* nymphs decreased significantly by 59% in potatoes and 66% in nightshade compared with the closed cages for both years of the experiment. Because parasitized psyllids were not observed with these cage experiments, generalist arthropod predators may have been responsible for the decreases in *B. cockerelli*. The results from this study open new possibilities of research regarding *B. cockerelli* management options and research avenues with natural enemies for this pest. As has been seen in other systems, the applications of pesticides could be timed to minimize the impact on natural enemies and the choice of selective compounds could potentially conserve the natural enemy groups we found feeding on psyllids (Rutledge et al. 2004). Cultural control practices, enhancement of the environment, and other conservation practices for beneficial insects (Van Driesche et al. 2008) should be investigated to improve management of *B. cockerelli* in solanaceous crops.

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