

Dynamics of Predation on *Lygus hesperus* (Hemiptera: Miridae) in Alfalfa Trap-Cropped Organic Strawberry

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Abstract

Alfalfa (*Medicago sativa* L.) (Fabales: Fabaceae) can be strategically planted as a trap crop for *Lygus* spp. in California's organic strawberry fields. Alfalfa has been shown to attract both *Lygus* spp. and, in turn, a *Lygus*-specific parasitoid, *Peristenus relictus* (Ruthe) (Hymenoptera: Braconidae). However, the impact of alfalfa trap-cropped strawberries on the *Lygus* spp. predator complex is unknown. Here we identify key predators of *Lygus* spp. found in organic strawberry. First, a general survey was conducted at an organic, non-trap cropped strawberry farm, to quantify predator abundance and to qualitatively assess their feeding activity on *Lygus* spp. We identified the 11 most abundant predator taxa present and, by using a *Lygus*-specific PCR assay, determined that about 18% of the insects and spiders contained *Lygus* spp. remains in their guts. We then conducted a study to examine alfalfa's role in conserving the most relevant predators in trap-cropped organic strawberries. Specifically, we quantified predator abundance and qualitatively measured predator feeding activity (by gut analysis) on *Lygus* spp. collected in strawberry plots either lacking or containing an alfalfa trap crop. Data revealed that some predator taxa, including the numerically dominant predator, *Orius tristicolor* (White) (Hemiptera: Anthocoridae), aggregated in alfalfa trap crops. The gut content analyses revealed that insect and spider predators collected from the alfalfa trap crop had a significantly higher proportion of their population containing *Lygus* spp. remains than those collected from nearby rows of strawberries. These results suggest that alfalfa trap cropping might be a useful tactic for conserving the biological control services of generalist predators in organically grown strawberries in California.

Key words: predator gut analysis, biological control, cultural control

The strawberry industry in the United States is concentrated in California, where 91% of the 1.3 billion kilograms of strawberries produced nationally in 2014 were grown (Marzolo 2015). Strawberry acreage in Monterey County, which is California's leading strawberry producer (California Department of Food and Agriculture 2017), has doubled from 1960 to 2014, while the cash value per acre has increased 12-fold over the same period (Tourte et al. 2016). Certified organic strawberry acreage statewide increased by 427% from 2000 to 2012 and constituted 11% of total strawberry acreage by 2017 (Tourte et al. 2016, California Strawberry Commission 2017).

Among the members of the *Lygus* species complex found in California strawberry, *Lygus hesperus* Knight (Hemiptera: Miridae), or western tarnished plant bug, is most common (Pickett et al. 2009) and is considered a key pest in reducing fresh market yields (Strand

2008). *Lygus* spp. (hereafter referred to as *Lygus*) feeding on the seed-like structures of immature strawberries, known as achenes, causes cosmetic fruit damage known as 'cat facing'. Such feeding damage deforms the fruit's appearance to such an extent that it becomes unmarketable (Handley and Pollard 1993). Current *Lygus* management challenges, such as insecticide resistance in local *Lygus* populations (Joseph and Bolda 2016), and a dearth of organically compliant management options, warrant investigation of alternative control strategies.

The strategic placement and arrangement of a preferred plant host (trap crop) in the vicinity of a high-value cash crop (e.g., strawberries) can concentrate pest distributions around that preferred host (Potting et al. 2005, Shelton and Badenes-Perez 2006, Gurr et al. 2017). For instance, to better manage *Lygus* along the California Central Coast, some organic strawberry growers have

integrated alfalfa trap crops in a variety of spatial arrays and acreage allotments, including intercropping alfalfa every 50th row (i.e., ~2% of total acreage), perimeter trap crops along field-edge rows, and/or bed-end plantings of alfalfa around individual blocks. As *Lygus* adults and nymphs are much more abundant in alfalfa when compared with associated strawberry rows, growers can conveniently target and efficiently mechanically remove this pest from alfalfa using tractor-mounted vacuums (Swezey et al. 2007, 2013).

The aggregated distributions of *Lygus* found in alfalfa also provide a favorable habitat for *Peristenus relictus* (Ruthe) (Hymenoptera: Braconidae), an introduced parasitoid of *Lygus* (Pickett et al. 2009). We recently examined the population dynamics and dispersal characteristics of *Lygus* and *P. relictus* in an alfalfa trap-cropped organic strawberry farm (Swezey et al. 2013, 2014). Those studies illustrated how trap cropping could facilitate conservation biological control, as *Lygus* abundance, parasitoid abundance, and parasitism rates were all higher in alfalfa and adjacent strawberry rows, relative to the rest of the strawberry field. Because of the spatial concentrations of *Lygus* prey in alfalfa trap crops, this management system also creates a conservation opportunity with respect to generalist predators.

We report here on two separate studies designed to identify common predators of *Lygus* in organic strawberry and illustrate the effects of high prey concentrations found in trap crops on predation frequency. We first characterized arthropod predators inhabiting an organic strawberry farm by quantifying their presence and examining their stomach contents to detect the presence of *Lygus* remains, which helps clarify the utility of generalist predators (Hagler et al. 1992, Unruh et al. 2008). We then examined alfalfa's role in conserving the most relevant generalist predators in this cropping system. Specifically, do higher *Lygus* (prey) densities found in alfalfa promote improved predation by the native predator community inhabiting organic trap-cropped strawberries? We hypothesized that: 1) *Lygus* and its predaceous natural enemies would aggregate in the alfalfa, and 2) that a higher proportion of the predators collected in the alfalfa would contain *Lygus* remains in their gut contents compared with those collected in the strawberries.

Materials and Methods

Lygus and Predator Survey in Non-Trap-Cropped Strawberries

Study Site

Predators were surveyed within a single 1 ha strawberry field located within the 60 ha multi-crop organic educational farm ALBA (Agriculture and Land-Based Training Association) in Salinas, CA (30° 36' 36.80 N; 121° 32' 14.17 W). First year 'Albion' strawberry beds were planted on 122 cm centers with plastic mulch. Beds were 46 cm wide, 30 cm tall, and were drip irrigated and fertilized with a single subsurface drip tape. The farm was registered and certified under the provisions of the California Organic Products Act of 2003, the California regulatory and enforcement mechanism for the federal Organic Food Production Act of 1990. Certification was provided by California Certified Organic Farmers, Santa Cruz, CA.

Arthropod Sampling Procedure

Arthropods were collected at ALBA on 14 August and 10 September 2012. The 1 ha strawberry field was divided into four 0.25 ha quadrants. In each quadrant, six 99-m-long strawberry rows were randomly selected for *Lygus* and predator collection. Collections were made using a handheld vacuum suction device (Stihl BG75

leaf blower) fitted with a 13 cm diameter insect-netted intake orifice. Each vacuum sample consisted of 100 one-second suction points directed at strawberry flowers and taken from a continuous line walked along the length of a strawberry row. Upon collection, arthropod samples were transferred to Ziploc bags and immediately placed in a cooler containing dry ice to halt their metabolic process. Samples were stored in -80°C freezers once we returned to the laboratory. Arthropods in each sample were identified and counted. As arthropod densities obtained on the two sample dates were very similar, data from both dates were pooled. The average number (\pm SEM) of *Lygus* and each predator taxa collected in the 48 vacuum samples was then determined.

Predator Gut Content Analysis

Due to time and budget constraints, it was not practical to examine the gut contents of every field-collected predator for the presence of *Lygus* remains. As such, we decided prior to the study, to cap the number of predators we examined for prey remains to approximately 500 individuals. For the readily abundant species (i.e., *O. tricolor*), we capped the number examined at five individuals per sample. Then, for the less abundant species, we arbitrarily chose a proportion of the population for analysis until we approached our cap of 500 individuals. The *Lygus*-specific PCR assay used to detect prey remains in the predator's guts is described in detail by Hagler and Blackmer (2013).

Lygus and Predator Survey in Alfalfa Trap-Cropped and Non-Trap-Cropped Strawberry Treatments

Study Site

This study was conducted in 2012 and 2013 at a 40 ha insecticide-free organic farm in Prunedale, CA (36° 45' 00.22 N; 121° 38' 43.55 W). The study site was partitioned into four rectangular blocks that were approximately 1.1 ha in size. Each block had four to five single-bed alfalfa trap crops (Ameristand 802 or Ameristand 901 nondormant alfalfa varieties) separated by 49 rows of 'Albion' strawberry. Within each block, trap crop and no trap crop treatments had main treatment rows of either alfalfa (trap crop treatment) or a 'control' row of strawberry, respectively. Adjacent to each of the main treatment rows were strawberry rows grouped into the following sampling treatments (zones) based on their proximity to either main row: rows 1–4, rows 7–10, and rows 13–16, respectively (Fig. 1). Arthropods (*Lygus* and predators) were collected using 100-suction samples (as described above) from each alfalfa trap crop row or strawberry control row and from the four rows within each of the associated sampling zones; i.e., 25 suction samples per row. Collections were made on 20 June 2012 and 24 July 2012 and 2 July 2013 and 16 August 2013. Arthropods were handled, stored, and processed as described above.

Statistical Analysis

Lygus and the five most commonly-collected predator taxa from the Prunedale strawberry site were selected for treatment comparisons. The predator species examined included the minute pirate bug (*Orius tricolor* (White) (Hemiptera: Anthracoridae)), big-eyed bug (*Geocoris punctipes* (Say) (Hemiptera: Geocoridae)), damsel bug (*Nabis alternatus* Parshley (Hemiptera: Nabidae)), dwarf spider (*Erigone* sp., *Tenuiphantes* sp.), and tangle-web spider (*Theridion* spp.).

Arthropod counts obtained from both sample dates were pooled within each year. *Lygus* and *O. tricolor* were readily encountered in our vacuum samples, and their counts were analyzed using

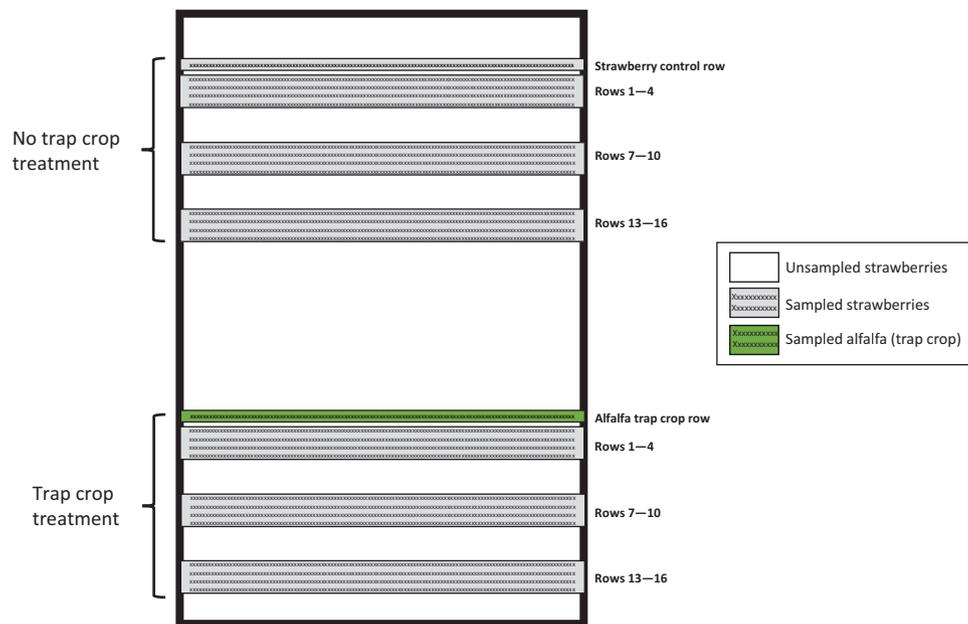


Fig. 1. Diagram of a typical block (1 of 4) depicting the location of the various vacuum sampling zones (rows) in plots consisting of only strawberries (no trap crop treatment present) or plots containing an alfalfa trap crop.

a generalized linear mixed model in the SAS procedure GLIMMIX (SAS 2012). Because conditional models for the *Lygus* analyses did not achieve convergence, generalized estimating equations (GEE) were used to fit marginal models. Fixed effects were crop treatment (no trap crop and trap crop) and sampling zone. The block by treatment \times date interaction represented the main plot experimental unit and was included as a random effect. A negative binomial distribution was used, and degrees of freedom were calculated using the Kenward-Roger adjustment. When the treatment by sampling zone interaction was non-negligible, simple effects of each effect were examined using the SLICE option of the LSMEANS statement. The *Orius* numbers were higher than counts of *Lygus*, which permitted estimation of conditional models using Laplace estimation. These models also provided stable estimates of block and date covariances, which were included as random effects. As in the *Lygus* models, the block by treatment \times date interaction was included as the error term for the main plot effect of trap crop or no trap crop treatment. In both analyses, comparisons among means representing the simple effects were adjusted for multiplicity using the ADJUST=SIMULATE option. Count data are presented as the inverse link of the model estimated mean (\pm SEM) number of *Lygus* and *Orius* in each vacuum sample.

Sample counts of the other predator taxa were sparse and characterized by too many zero counts to allow analysis by linear models. Instead, for each taxon, patterns in the distributions of integer counts across sample zones were contrasted between no trap crop and trap crop treatments using contingency tables (SAS 2012). In these tables, sampling zones formed columns, and crop treatments formed rows. Counts from each year were analyzed separately. The tables were stratified by sample date and block, which served roles analogous to blocks in a linear model. In a stratified analysis, inconsistencies in the patterns among strata penalize the test (increase the *P*-values) compared with a test based only on marginal counts. Because sampling zones were ordinal but unevenly spaced, the Mantel-Haenszel row means score statistic (Q_{SMH}) was used, and scoring used standardized midranks (the SCORES=MODRIDIT option; Stokes et al. 2012). When a significant difference was indicated by the row mean score statistic, cell chi-square and expected values were used

as informal guides to interpret the nature of the difference. Also, the distributions of counts among sampling zones within the main crop treatments were examined by year to assess whether disproportionate counts of a given taxa occurred in any particular sampling zone. Analyses were similar to those comparing the distributions of counts between treatments, except table columns were formed by the counts representing each sample, and table rows were formed by the sampling zones. Because both rows and columns were ordinal and unequally spaced, the Mantel-Haenszel nonzero correlation statistic (Q_{CSMH}) was used with standardized midrank scoring.

Predator Gut Content Analysis

Again, due to time and budget constraints, predator gut content examinations were performed only on randomly selected members of each of the focal predator taxa as described above (note that the overall total of predators examined for this study was capped at approximately 1,000 individuals). The number of predators collected and assayed was tallied for each taxon, and the frequency of predators containing *Lygus* DNA was calculated. Significant differences in feeding frequencies among sampling zones within and between treatments were determined by the *z*-test with Yates correction for continuity (Glantz 1997).

Results

Lygus and Predator Survey in Non-Trap-Cropped Strawberries

Lygus were very abundant in the organic strawberry field at ALBA, with an average of 39.7 ± 2.9 individuals (nymphs and adults combined) collected in each sample ($n = 48$ vacuum samples). The densities of the 11 most abundant predator taxa collected at ALBA are given in Table 1. Minute pirate bugs, consisting almost entirely of *O. tristicolor*, comprised 64% of the total predator fauna. Tangle-web spiders and damsel bugs were the next most abundant taxa, comprising 13 and 10% of the total predator fauna, respectively.

Table 1. Arthropod predators collected with their corresponding gut content analysis results from an organic strawberry field in Salinas, CA

Class	Order	Family	Predominate taxon ^a	Common name	Predator abundance			PCR assay results		
					No. collected	Mean	SE	No. assayed	No. positive	% positive
Insecta	Hemiptera	Anthocoridae	<i>Orius tristicolor</i>	Minute pirate bug	1,976	41.2	2.3	116	21	18.1
		Nabidae	<i>Nabis alternatus</i>	Damsel bug	320	6.7	0.7	82	16	19.5
		Geocoridae	<i>Geocoris punctipes</i>	Big-eyed bug	103	2.1	0.5	50	9	18.0
	Neuroptera	Chrysopidae	<i>Chrysoperla carnea</i>	Green lacewing	82	1.7	0.2	24	2	8.3
		Insecta total				2,481	12.9	1.3	272	48
Arachnida	Araneae	Theridiidae	<i>Theridion</i> spp.	Tangle-web spider	398	8.3	0.8	75	8	10.7
		Linyphiidae	<i>Erigone</i> spp., <i>Tenuiphantes</i> sp.	Dwarf spider	39	0.8	0.2	17	3	17.6
		Tetragnathidae	<i>Tetragnatha laboriosa</i>	Long-jawed orb weaver spider	7	0.2	0.1	7	1	14.3
		Thomisidae	<i>Misumenops</i> sp.	Crab spider	150	3.1	0.3	63	20	31.7
	Opiliones	Lycosidae	<i>Pirata</i> sp.	Wolf spider	7	0.2	0.1	7	0	0.0
		Salticidae	<i>Eris</i> sp.	Jumping spider	11	0.2	0.1	9	1	11.1
		Phalangium	Unknown	Harvestman	11	0.2	0.1	9	1	11.1
		Arachnida total				623	1.9	0.2	187	34
Grand total					3,104	5.9	0.6	459	82	17.9

^aPredators assayed included both immature and adult lifestages, except for *C. carnea* (only the larval stage was examined).

Overall, the proportion of insects and spiders containing *Lygus* remains were almost identical at 17.6 and 18.2%, respectively (Table 1). The minute pirate bug, damsel bug, and big-eyed bug were the three most common insect predators encountered. Approximately 18% of each of these true bug species contained *Lygus* remains in their gut (Table 1). Of the examined hunting spiders (Thomisidae, Salticidae, and Lycosidae), 26.6% had *Lygus* DNA in their guts. Of the examined web-building spiders (Linyphiidae, Theridiidae, and Tetragnathidae), 12.1% had detectable *Lygus* remains. In addition, 11.1% of Opiliones (harvestmen) tested positive for *Lygus* remains in their guts.

Lygus and Predator Survey in Trap-Cropped and Non-Trap-Cropped Strawberry Treatments

Lygus (*Lygus* Bug)

Analyses of *Lygus* nymphal counts obtained in 2012 indicated significant differences between the main treatments ($F = 33.28$; $df = 1, 12.15$; $P < 0.001$) and sampling zones within the treatments ($F = 8.42$; $df = 3, 76.8$; $P < 0.001$); however, treatment by sampling zone interactions indicated the effect of sampling zone was conditional on the main crop treatment ($F = 7.86$; $df = 3, 76.8$; $P < 0.001$). The examination of simple effects between treatments within sampling zones indicated a highly significant difference in *Lygus* density between the main treatment alfalfa (trap crop) row and the control strawberry row ($F = 46.48$; $df = 1, 79.36$; $P < 0.001$). On average, 1.63 ± 0.63 and 31.3 ± 5.94 *Lygus* nymphs were collected in control strawberry and alfalfa rows (Fig. 2a and b), respectively. There was also a significant difference in *Lygus* nymph density between rows 1–4 of strawberries associated with the main treatments ($F = 6.82$; $df = 1, 77.19$; $P = 0.01$). An average of 1.50 ± 0.49 and 4.25 ± 0.96

nymphs were captured in the no trap crop treatment and trap crop treatment (Fig. 2a and b), respectively. There were no significant differences in *Lygus* density between the main treatments in rows 7–10 ($F = 0.80$; $df = 1, 78.32$; $P = 0.38$) or rows 13–16 ($F = 1.25$; $df = 1, 67.01$; $P = 0.27$).

Tests of the simple effects in 2012 indicated no significant differences in *Lygus* nymph density among the sampling zones within the no trap crop treatment ($F = 0.37$; $df = 3, 67.05$; $P = 0.78$). In other words, the *Lygus* population was evenly distributed, at very low densities, among the various sampling zones (Fig. 2a). However, there were highly significant differences in *Lygus* densities among the sampling zones in the trap crop treatment ($F = 31.95$; $df = 3, 55.22$; $P < 0.001$). As expected, there were significantly more *Lygus* collected from the alfalfa trap crop row than from the adjacent strawberry rows ($P < 0.001$; Fig. 2b). Nymphal densities from the other sampling zones (strawberries) within the trap crop treatment were not statistically distinguishable (Fig. 2b; $0.22 \leq P \leq 0.85$).

Overall, the trends in the *Lygus* densities in 2013 were similar to those in 2012; effects of the main treatment ($F = 9.49$; $df = 1, 14$; $P < 0.008$) and sampling zone ($F = 10.84$; $df = 3, 51.2$; $P < 0.001$) were significant along with the treatment by sampling zone interaction ($F = 9.64$; $df = 3, 51.2$; $P < 0.001$). Again, tests of simple effects of sampling zone indicated no differences within the no trap crop treatment (Fig. 2c; $F = 0.08$; $df = 3, 48.71$; $P = 0.97$). In contrast, significant nymphal differences were indicated within the alfalfa trap crop treatment (Fig. 2d; $F = 24.86$; $df = 3, 39.01$; $P < 0.001$). Comparisons among sampling zones in the trap crop treatment indicated greater numbers of *Lygus* collected from the alfalfa trap crop row (36.13 ± 8.35 nymphs per sample) when compared with sampled strawberry rows ($P < 0.001$). Nymphal abundance from trap-cropped strawberry rows (1.8 – 4.1 per sample) were statistically

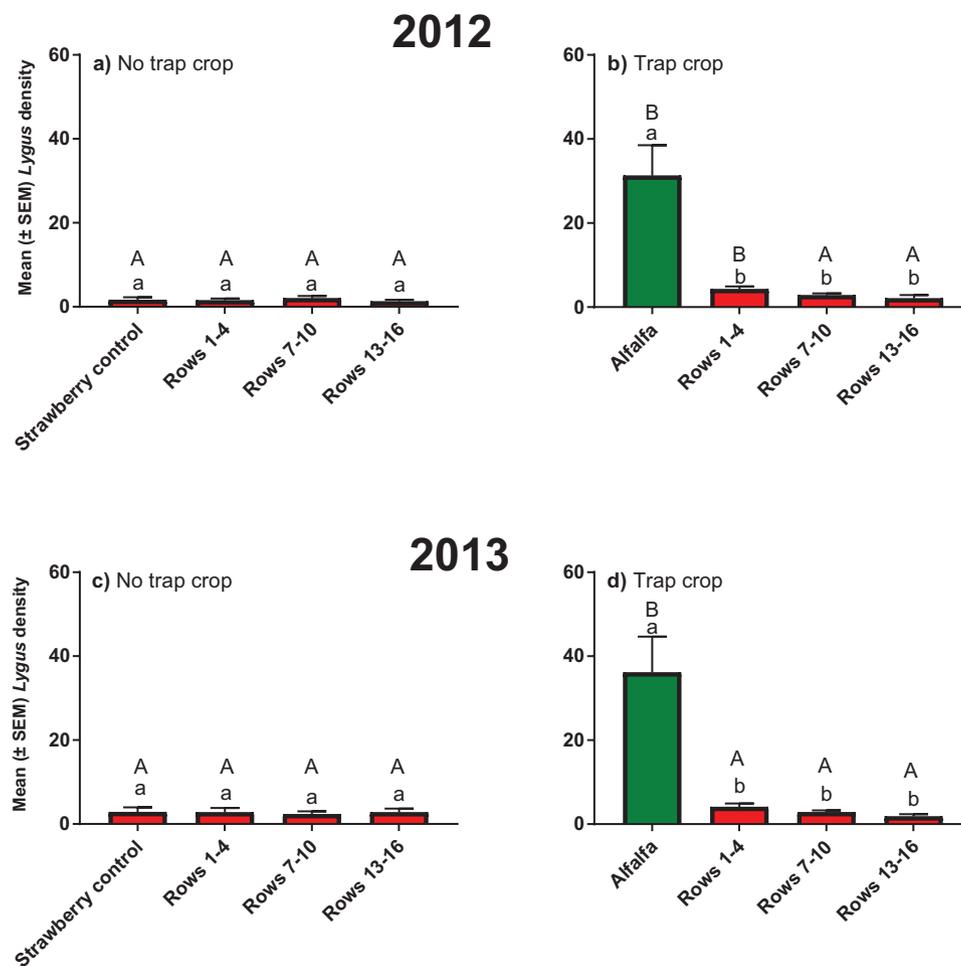


Fig. 2. Mean (\pm SEM) *Lygus* nymph abundance per vacuum sample taken on two dates in 2012 and 2013 from field plots without and with an alfalfa trap crop. Means within each main treatment followed by a different lower case letter are significantly different and means between the main treatment zones (i.e., trap crop and control) followed by different uppercase letter are significantly different.

equivalent (Fig. 2d; $0.31 \leq P \leq 0.83$). Simple effects examining differences between treatments within sampling zones indicated a significant effect for only nymphs in the alfalfa trap crop row, which were significantly higher than in the control strawberry row in the no trap crop treatment (main treatment rows, $F = 42.40$; $df = 1$, 38.49; $P < 0.001$; rows 1–4, $F = 0.82$; $df = 1$, 55.92; $P = 0.37$; rows 7–10, $F = 0.18$; $df = 1$, 46.69; $P = 0.67$; rows 13–16, $F = 0.76$; $df = 1$, 38.2; $P = 0.39$).

O. tristicolor (Minute Pirate Bug)

Analyses of the *O. tristicolor* counts obtained from 2012 indicated significant treatment ($F = 5.91$; $df = 1$, 10; $P = 0.04$) and sampling zone effects ($F = 7.13$; $df = 3$, 66; $P < 0.001$), but also a significant treatment by sampling zone interaction ($F = 10.08$; $df = 3$, 66; $P < 0.001$). This interaction indicates that the effect of the trap crop treatment was conditional on sampling zone. While tests of simple effects indicated no differences in *O. tristicolor* densities among sampling zones within the no trap crop treatment (Fig. 3a; $F = 0.54$; $df = 3$, 66; $P = 0.65$), a highly significant difference between the sampling zones was indicated within the trap crop treatment (Fig. 3b; $F = 17.49$; $df = 3$, 66; $P < 0.01$). Comparisons among counts corresponding to sampling zones within the trap crop treatment indicated higher numbers of *O. tristicolor* in the alfalfa trap crop row compared with the strawberry sampling rows ($P < 0.01$),

but no other differences between strawberry rows were detected ($0.90 \leq P < 1.00$).

Simple effects comparing corresponding sampling zones between treatments indicated highly significant differences in *O. tristicolor* populations between the strawberry control row in the no trap crop treatment and the alfalfa row in the trap crop treatment ($F = 28.23$; $df = 1$, 66; $P < 0.01$). Specifically, the *O. tristicolor* population was much higher in the alfalfa row in the trap crop treatment (109.5 ± 41.7 per sample) than the control strawberry row in the no trap crop treatment (27.4 ± 10.6 per sample; Fig. 3a and b). Differences in *O. tristicolor* densities for other sampling zones were not demonstrated between the two main treatments (rows 1–4, $F = 0.94$; $df = 1$, 66; $P = 0.34$; rows 7–10, $F = 0.14$; $df = 1$, 66; $P = 0.71$; rows 13–16, $F = 0.38$; $df = 1$, 66; $P = 0.54$).

Overall, *O. tristicolor* densities were lower in 2013, but the statistical trends were identical (Fig. 3c and d) to 2012: effects of treatment, sampling zone, and their interaction were significant (treatment, $F = 7.88$; $df = 1$, 10; $P = 0.02$; sampling zone, $F = 6.76$; $df = 3$, 42; $P < 0.01$; treatment by sampling zone, $F = 8.71$; $df = 3$, 42; $P < 0.01$). Comparisons among sampling zones within the main treatments indicated significant differences only for the trap crop treatment ($F = 16.84$; $df = 3$, 42; $P < 0.001$; no trap crop, $F = 0.14$; $df = 3$, 42; $P = 0.93$). Within the trap crop treatment, *O. tristicolor* counts were significantly higher in the alfalfa trap crop than the

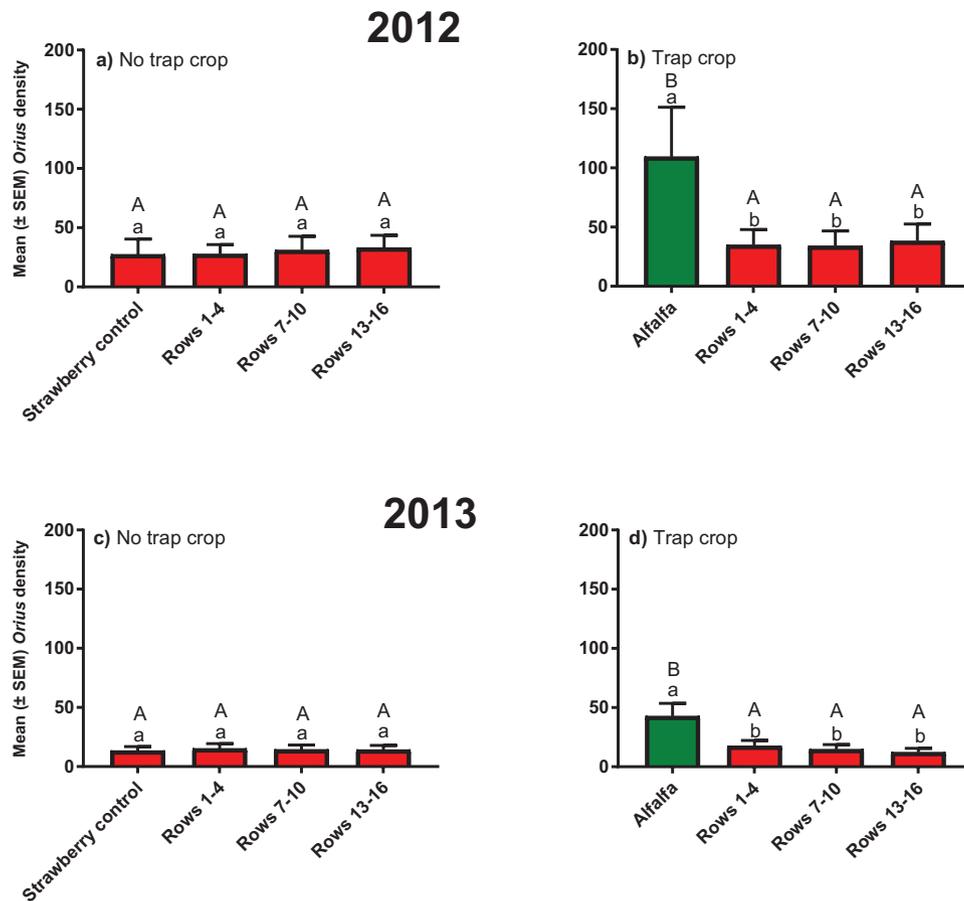


Fig. 3. Mean (\pm SEM) *Orius tristicolor* abundance (adults + nymphs) per vacuum sample taken on two dates in 2012 and 2013 from field plots without and with an alfalfa trap crop. Means within each main treatment followed by a different lower case letter are significantly different and means between the main treatment zones (i.e., trap crop and control) followed by different uppercase letter are significantly different.

other sampling zones (strawberries) ($P < 0.001$). Counts within the other strawberry sampling zones in the trap crop treatment were statistically equivalent ($0.30 \leq P \leq 0.82$). Comparisons of sample zones between treatments indicated a significantly higher population of *O. tristicolor* in the alfalfa trap crop row than in the strawberry control row ($F = 35.00$; $df = 1, 42$; $P < 0.001$). Similar differences in other sampling zones were not demonstrated (rows 1–4, $F = 0.48$; $df = 1, 42$; $P = 0.49$; rows 7–10, $F = 0.02$; $df = 1, 42$; $P = 0.90$; rows 13–16, $F = 0.48$; $df = 1, 42$; $P = 0.49$).

G. punctipes (Big-Eyed Bug)

In general, regardless of the sample zone, fewer than five *G. punctipes* were collected per vacuum sample during each sample date and year of the study. Comparisons of *G. punctipes* frequency distributions across sampling zones did not indicate differences between the no trap crop and trap crop treatments in either year of the study (2012, $Q_{SMH} = 0.89$, $df = 1$, $P = 0.35$; 2013, $Q_{SMH} = 0.00$, $df = 1$, $P > 0.99$) even though only 4.6 and 0% of the *G. punctipes* populations were captured in the alfalfa trap crop row in year 1 and year 2, respectively; compared with 11.1 and 22.1% in the strawberry control row of the no trap crop treatment. Examination of the distribution of *G. punctipes* counts among sampling zones within the no trap crop treatment likewise failed to detect a significant pattern in densities either year (year 1, $Q_{CSMH} = 0.63$, $df = 1$, $P = 0.43$; year 2, $Q_{CSMH} = 2.17$, $df = 1$, $P = 0.14$). However, significant patterns were detected within the trap crop treatment in both years (2012,

$Q_{CSMH} = 6.86$, $df = 1$, $P < 0.01$; 2013, $Q_{CSMH} = 4.37$, $df = 1$, $P = 0.04$). The pattern appeared to result from low counts (2012) or no counts (2013) of *G. punctipes* in the alfalfa row of the trap crop treatment. Specifically, in 2012, 62.5% of the vacuum samples in that zone yielded no *G. punctipes*, and in 2013, not a single individual (e.g., 100% of the counts were 0) was collected from the alfalfa. Only 12.5 to 37.5% of *G. punctipes* counts from samples collected from the other zones (various strawberry sampling zones) were zeros.

N. alternatus (Damsel Bug)

Analyses of the *N. alternatus* counts obtained from 2012 did not indicate differences between treatments in their distribution among sampling zones ($Q_{SMH} = 1.96$, $df = 1$, $P = 0.16$) or among counts from different sampling zones within the main treatments (no trap crop, $Q_{CSMH} = 0.01$, $df = 1$, $P = 0.91$; trap crop, $Q_{CSMH} = 0.97$, $df = 1$, $P = 0.32$). This was undoubtedly due to the very low collection rates of *N. alternatus* in the various sampling locations. Specifically, no damsel bugs were collected in the strawberry control row of the no trap crop treatment in 2012 and in most other cases, less than one individual was collected per sample in the other sampling zones. However, the second year's analyses indicated higher frequencies of *N. alternatus* in the alfalfa row (45.4% of the total) and rows 1–4 (31.8% of the total) of the trap crop treatment, compared to those locations in the no trap crop treatment (strawberry control row, 17.5%; rows 1–4, 12.5%). In addition, a higher percentage of total bugs were collected from sample rows 7–10 in the no trap crop

treatment (52.5% of the total population) compared with the same location of the trap crop treatment (9.1%) ($Q_{SMH} = 5.77$, $df = 1$, $P = 0.02$). Also in 2013, no pattern in the distributions of *N. alternatus* counts among sampling zones in the no trap crop treatment were observed ($Q_{CSMH} = 0.13$, $df = 1$, $P = 0.72$). In contrast, in the trap crop treatment, the frequency of zero counts from the alfalfa treatment row (12.5%) was lower than expected and collections of single damsel bugs from rows 1–4 were more frequent than expected (62.5%) ($Q_{CSMH} = 7.75$, $df = 1$, $P = 0.005$). The apparent inconsistencies between results from 2012 and 2013 may have resulted from higher statistical power in the tests in 2013 by virtue of the higher damsel bug populations.

Theridion spp. (Tangle-Web Spider)

Although only one tangle-web spider was collected from the alfalfa row in the trap crop treatment in both years of the study (compared with a total of 49 collected in all the other strawberry rows), the analyses did not demonstrate a difference between treatments in the numbers of spiders collected from the various sampling zones (2012, $Q_{SMH} = 1.30$, $df = 1$, $P = 0.25$; 2013, $Q_{SMH} = 0.18$, $df = 1$, $P = 0.67$). Analyses of the distributions of tangle-web spider counts among sampling zones within the main crop treatments also failed to indicate significant patterns of collection (2012, no trap crop, $Q_{CSMH} = 1.40$, $df = 1$, $P = 0.24$; trap crop, $Q_{CSMH} = 2.22$, $df = 1$, $P = 0.14$; 2013, no trap crop, $Q_{CSMH} = 0.22$, $df = 1$, $P = 0.64$, trap crop, $Q_{CSMH} = 1.71$, $df = 1$, $P = 0.19$). In these latter analyses, zero counts in all sampling zones were common in both treatments (2012, no trap crop 25–50%, trap crop, 50–87.5%; 2013, no trap crop 25–50%, trap crop 25–100%), and each non-zero sample tended to contain multiple tangle-web spiders. Therefore, either no pattern in tangle-web spider distribution was associated with treatment and among sample zones, or patterns of distribution were not consistent among strata (blocks and dates).

Linyphiidae (Dwarf Spider)

No significant differences between main crop treatments in the distributions of dwarf spiders among sampling zones were demonstrated in either year of the study (2012, $Q_{SMH} = 2.60$, $df = 1$, $P = 0.11$; 2013, $Q_{SMH} = 2.64$, $df = 1$, $P = 0.10$), despite numerically lower percentages of zero counts in the alfalfa row of the trap crop treatment when compared to the control strawberry row of the no trap crop treatment in both years (trap crop vs. no trap crop; 2012, 20.0 vs. 39.3%; 2013, 5.1 vs. 28.7%). There were significant differences detected in the distribution of dwarf spiders among the sampling zones in 2012 for the no trap crop treatment ($Q_{CSMH} = 6.28$, $df = 1$, $P = 0.01$) and 2013 for the alfalfa trap crop treatment ($Q_{CSMH} = 3.74$, $df = 1$, $P = 0.05$). Marginal totals (i.e., row and column totals yielded from the contingency table analysis) suggested higher than expected incidence of dwarf spiders in the strawberry control row in 2012, and lower than expected incidence in the alfalfa trap crop row in 2013. However, there were no differences detected in the distributions of counts of dwarf spiders among the sampling zones in 2012 of the alfalfa trap crop treated fields ($Q_{CSMH} = 0.07$, $df = 1$, $P = 0.80$) or in 2013 of the no trap crop treatment ($Q_{CSMH} = 0.19$, $df = 1$, $P = 0.66$).

Predator Gut Content Examinations for the Presence of *Lygus* Remains

A summary of the gut content examination results obtained for each predator taxa is given in Table 2. A total of 693 insect predators, from three hemipteran taxa, were analyzed for the presence of *Lygus* remains. The proportion of insect predators containing

Lygus remains was about the same (not significantly different) for those insect predators collected in the various sampling zones of the no trap crop treatment. The frequencies of positive assay reactions for *Lygus* remains ranged from 6.8% in rows 13–16 to 13.1% in the strawberry control row (Fig. 4a). However, there was a significant difference in the proportion of insect predators containing prey remains for those predators collected in the various sampling zones of the alfalfa trap crop treatment. Specifically, the proportion of individuals (20%) containing *Lygus* prey remains was significantly higher ($P < 0.01$) for the those collected in the alfalfa trap crop and the adjacent sampling zone (rows 1–4; 15.4% of the population) than in rows 7–10 and rows 13–16; Fig. 4b).

A total of 206 web-building spiders were analyzed for the presence of *Lygus* remains (Table 2). As with the insect predators, the proportion of spiders containing *Lygus* remains was not significantly different for those collected in the various collection zones of the no trap crop treatment (Fig. 5a). The proportion of the spider population containing *Lygus* remains ranged from 0% in rows 1–4 to 10.0% in rows 13–16. For those spiders collected in the trap crop treatment, the highest proportion (22.0%) containing *Lygus* remains were obtained from the alfalfa trap crop row. The spiders collected from the alfalfa row had a significantly higher proportion of their population ($P = 0.04$) containing *Lygus* remains than those collected from the adjacent strawberry rows of the trap crop treatment (Fig. 5b).

Discussion

The general predator survey revealed a variety of predaceous natural enemies inhabiting an organic strawberry field. The most common insect predators were *O. tristicolor*, *N. alternatus*, and *G. punctipes*, which is very similar to the hemipteran assemblages found in alfalfa (Clancy and Pierce 1966, Hagler et al. 1992) and cotton (Naranjo et al. 2004, Hagler 2011, Hagler and Blackmer 2013). *O. tristicolor* was most prominent in strawberry, constituting 80% of all collected insect predators. The high abundance of *O. tristicolor* may be attributable to the diversity of relevant food sources (other than *Lygus*) available during the extensive strawberry harvest season, such as thrips, aphids, mites, eggs and pollen (Salas-Aguilar and Ehler 1977). There was also a wide variety of arachnids inhabiting strawberry, which included six spider families and harvestmen. Theridiids, thomisids, and linyphiids were most commonly collected. While all six families of this spider community are also present in cotton, family composition is quite different, as the commonly encountered spiders in strawberry were seldom collected in cotton, and vice versa (Hagler 2011). This survey in strawberry identified a diverse predator community including four species of insects and six families of arachnids that consumed *Lygus* of one or more life stage.

Predation, which was documented in 17.6% of collected insects and 18.2% of collected spiders, was likely bolstered by high *Lygus* nymph densities and a lack of management-related disturbances (e.g., vacuuming or insecticide applications). Nevertheless, detection frequency of *Lygus* remains (10–30%) in the digestive system of the various spider species was very similar to *Lygus* prey detection rates in cotton (Hagler and Blackmer 2013). These predation frequencies actually represent a very conservative estimate of predation, as viable prey DNA is only recognizable for a limited time after a predation event. In a prey retention study, *L. hesperus* remains were no longer detectable via PCR from a suite of insect and spider predators 12 to 48 h after consumption (Hagler and Blackmer 2013).

This community of natural enemies is likely capable of affecting pest population growth rates by collectively targeting all life

Table 2. Summary statistics for the various predator taxa collected from a trap-cropped organic strawberry farm in 2012 and 2013, located in Prundale, CA

Class	Order	Family	Predominate taxon	Main treatment	Sample row	No. collected	No. assayed	No. positive	% positive		
Insecta	Hemiptera	Anthororidae	<i>Orius tristicolor</i>	No trap crop	Strawberry control	412	69	8	11.59		
					Rows 1–4	612	64	5	7.81		
					Rows 7–10	689	58	3	5.17		
					Rows 13–16	698	62	5	8.06		
					Trap crop	Alfalfa	1,296	81	13	16.05	
						Rows 1–4	670	55	9	16.36	
				Geocoridae	<i>Geocoris punctipes</i>	No trap crop	Strawberry control	43	11	2	18.18
							Rows 1–4	56	17	1	5.88
							Rows 7–10	78	26	2	7.69
						Trap crop	Rows 13–16	76	22	0	0.00
							Alfalfa	5	3	1	33.33
							Rows 1–4	54	14	1	7.14
		Nabidae	<i>Nabis alternatus</i>	No trap crop	Strawberry control	7	4	1	25.00		
					Rows 1–4	8	6	2	33.33		
					Rows 7–10	25	9	2	22.22		
					Rows 13–16	8	4	1	25.00		
					Trap crop	Alfalfa	20	16	6	37.50	
				Rows 1–4		14	9	2	22.22		
				Rows 7–10		4	1	0	0.00		
				Rows 13–16		10	8	0	0.00		
				Insecta total		6,187	693	69	9.96		
				Arachnida	Araneae	Linyphiidae	Erigone spp. Tenuiphantes sp.	No trap crop	Strawberry control	68	23
		Rows 1–4	60						20	0	0.00
Rows 7–10	61	13	0						0.00		
Rows 13–16	65	21	3						14.29		
Trap crop	Alfalfa	24	9						2	22.22	
	Rows 1–4	74	17						0	0.00	
Therididae	Theridion spp.	No trap crop	Strawberry control					17	9	1	11.11
			Rows 1–4					14	10	0	0.00
			Rows 7–10					11	8	1	12.50
		Trap crop	Rows 13–16					23	9	0	0.00
			Alfalfa					0	na	na	na
			Rows 1–4					29	14	1	7.14
Rows 7–10	25	12	1			8.33					
Rows 13–16	13	6	0			0.00					
Arachnida total	636	206	10			4.85					
Grand total	6,823	899	79			8.79					

stages of a *Lygus* population. *Lygus* eggs are attacked both by predators and the parasitoid *Anaphes iole* (Norton and Welter 1996). By using an *L. hesperus* egg-specific gut assay, Hagler et al. (1992) reported that 35.0, 19.7, and 6.3% of field-collected *N. alternatus*, *G. punctipes*, and *O. tristicolor* fed on *L. hesperus* eggs in alfalfa, respectively. Based on laboratory choice tests and gut content analyses, *Lygus* nymphs can be debilitated and consumed by both roaming or hunting insects (e.g., *Geocoris* spp.) and ambush predators (e.g., *N. alternatus*) (Leigh and Gonzalez 1976; Tamaki et al. 1978; Hagler and Cohen 1991; Hagler 2006, 2011). *Geocoris* spp. and *O. tristicolor* are both capable of consuming

smaller *Lygus* nymphs based on field cage studies in cotton (Zink and Rosenheim 2008) and alfalfa trap crops (unpublished data). Larger predators, on the other hand, such as *N. alternatus* and the hunting spider *Oxyopes salticus* (Oxyopidae), can capture and consume both *Lygus* nymphs (of all instars) and adults (Perkins and Watson 1972, Young and Lockley 1986, Hagler et al. 1992). While predation of all life stages is important for population management, top-down mortality of eggs and young nymphs is especially useful as a means of avoiding or reducing strawberry yield losses, as feeding by larger *L. hesperus* nymphs is especially damaging (Allen and Gaede 1963).

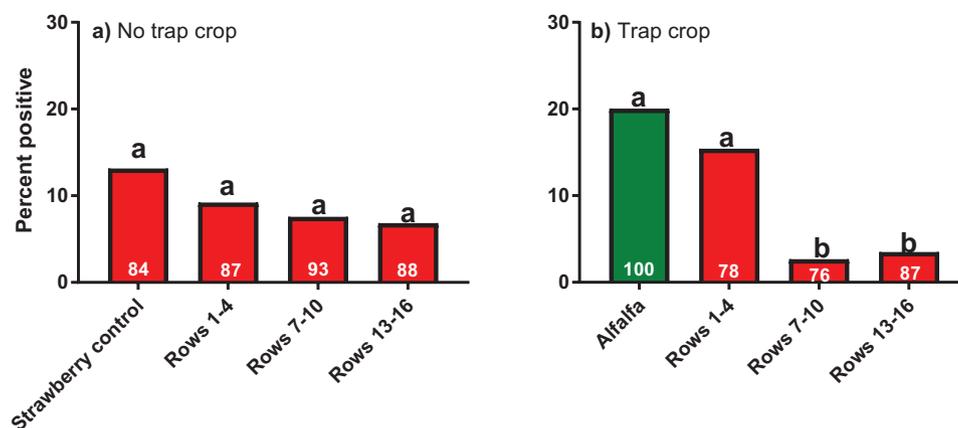


Fig. 4. Percentage of insect predators positive for the presence of *Lygus* remains in their guts. Means within each main treatment followed by a different lower case letter are significantly different as determined by the z-proportions test. The number inside each bar is the number of predators examined for the presence of *Lygus* prey remains.

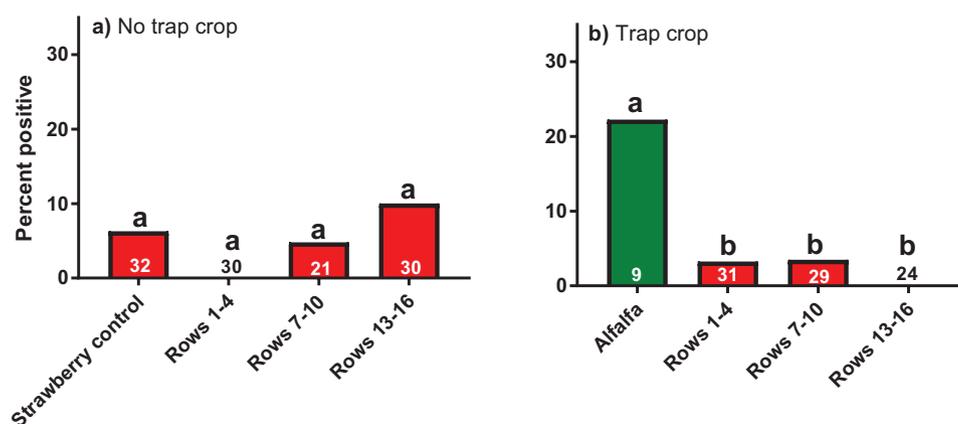


Fig. 5. Percentage of web-building spiders scoring positive for the presence of *Lygus* remains in their guts. Means within each main treatment followed by a different lower case letter are significantly different as determined by the z-proportions test. The number inside each bar is the number of predators examined for the presence of *Lygus* prey remains.

Generalist predators are important contributors to pest management, as shown by Symondson et al. (2002), who reported that generalist predators significantly reduced pest populations in 75% of reviewed field studies. More specifically, Zink and Rosenheim (2008) concluded that *Geocoris* spp. populations alone can depress seasonal *Lygus* nymphal densities in cotton. It should be noted, however, that generalist predators alone are not typically considered sufficient in suppressing pest pressure in strawberry beneath the low economic threshold of 1–2 *Lygus* nymphs per 20 plants (Strand 2008). While the predator community in strawberry does not represent a ‘silver bullet’ to pest management, it nonetheless provides an important source of *Lygus* mortality within balanced pest management programs. When compared with specialist natural enemies, populations of generalist predators can provide a more timely response to sudden pest buildups early in a growing season (Symondson et al. 2002). Using strawberry on the central California coast as an example, generalist predators establish populations during the spring by consuming alternate prey (e.g., mites, aphids, thrips, etc.) and are well-positioned to reduce *Lygus* population growth rates during early summer.

The study of *Lygus* and their associated predators in trap-cropped organic strawberry revealed high pest densities in alfalfa and consistently low *Lygus* densities in strawberries.

Lygus nymphs were about 15 times more abundant in alfalfa trap crops when compared with strawberry rows in either trap crop or no trap crop treatments. Similarly, about 67% of the *Lygus* nymph field population was aggregated in alfalfa trap crop rows, which constitute roughly 2% of farm acreage. These results are comparable to findings in Swezey et al. (2013). Previous laboratory and field studies have shown that *L. hesperus* has a preference for alfalfa (Blackmer and Cañas 2005) over other crops such as cotton (Sevacherian and Stern 1975) and strawberry (Swezey et al. 2007). In this study, *Lygus* densities in strawberry in both trap crop and non-trap crop treatments fell below the economic threshold of one nymph per 10 suction samples (Dara et al. 2012), and were generally consistent with spatial trends and treatment comparisons made by Swezey et al. (2007), which demonstrated a significant reduction of fresh market damage in trap-cropped strawberry rows.

The predominant arthropod taxa encountered in the trap cropping study was *O. tristicolor*, which comprised over 75% of the total evaluated predator population. *O. tristicolor*, and to a lesser extent, *N. alternatus*, demonstrated an aggregated response in alfalfa trap crops, likely in reaction to increased prey availability (i.e., high spatial concentrations of *Lygus*). Alfalfa trap crops used to manage the mirid pest *Creontiades dilutes* in Australia (Mensah and Khan 1997), had higher densities of generalist predators (e.g., *Nabis* sp., *Geocoris* sp., Lycosidae, Oxyopidae and Salticidae) when compared

with associated cotton (Mensah 1999). In California, Godfrey and Leigh (1994) demonstrated a strong association between *L. hesperus* nymphs and generalist predators (*O. tristicolor*, *Geocoris* spp. and *N. alternatus*) across various alfalfa trap crop treatments. Specifically, alfalfa that was harvested less frequently had higher densities of *L. hesperus* nymphs, which were significantly correlated with generalist predators (adults + nymphs) during both years of the study.

Given the previous examples of predator aggregation in alfalfa, the findings that *Geocoris* spp. and web-building spiders were less commonly collected in alfalfa trap crops than in the various strawberry sampling zones was unexpected. Underrepresented arthropod counts may be attributable to how they were collected from different portions of a plant canopy, rather than an actual paucity of predators in alfalfa. Given that the surface area of an alfalfa plant is much greater than that of a strawberry plant, the respective canopies were sampled differently; i.e., the entire strawberry canopy was sampled with vacuum suction, whereas only the upper canopy (e.g., the area in bloom) was exposed to suction in alfalfa. This effect was exacerbated by the comparatively small intake orifice of the hand-held vacuum used in this study, which has a diameter roughly one-third the size of either a standard sweep net or D-vac used in aforementioned alfalfa studies. Hence, collecting arthropods using this technique could result in an under-representation of species that were either evenly distributed on an alfalfa plant or were aggregated toward the lower portion of the canopy. For instance, it is likely that we regularly collected *Lygus* and minute pirate bugs in the alfalfa because these species tend to aggregate on flowers. *Lygus* are attracted to visual and volatile cues emitted by many different flowers, including alfalfa, and often preferentially oviposit on these reproductive structures (Blackmer et al. 2004, Blackmer and Cañas 2005, Williams et al. 2010, Hagler et al. 2016). *Orius* spp. readily feed on resources provided in or on the flower, such as pollen, nectar, thrips and *Lygus* eggs (Wong and Frank 2013). Conversely, *Geocoris* spp., which are often ground-dwelling predators (Crocker and Whitcomb 1980) and web-building spiders, which can aggregate (vertically) toward the middle and lower portions of a plant canopy (Nyffeler and Benz 1988, Fasola and Mogavero 1995), were seldom collected in alfalfa. In a 2013 pitfall trap study conducted at the same Prunedale farm as our present study, Biswas (2015) determined that theridiid spiders were more abundant in trap crops when compared with distant strawberry rows. Future studies are thus needed to develop a non-biased predator sampling scheme for these two plant types (e.g., proportionally timed vacuum samples based on plant biomass differentials).

Linyphiid dwarf spiders were not preferentially distributed to either alfalfa or strawberry, as evidenced by both suction samples in this study and pitfall traps (Biswas 2015). As agriculturally-relevant linyphiids construct sheet webs on or very near to the ground, plant architecture offered by either alfalfa or strawberry is likely suitable for prey capture (Thornhill 1983, Alderweireldt 1994). Since dwarf spiders are commonly encountered in California strawberry (Dara et al. 2012), understanding their preferences and behaviors will be especially useful in making more impactful management decisions.

Irrespective of relative sampled predator abundances in strawberry or alfalfa, these findings indicate a behavioral response by generalist predators to spatial aggregations of *Lygus* prey in the form of selective predation. Gut content analyses revealed that higher frequencies of true bugs (all three species combined) collected in alfalfa (20%) and adjacent strawberry rows 1–4 (15%) contained *Lygus* remains than similar specimens collected in strawberry rows 7–10 (2.6%) and 13–16

(3.5%). True bug predators have been reported to increase their feeding activity when exposed to greater prey densities (Propp 1982, Shrestha et al. 2004, Desneux and O’Neil 2008) that are generated through spatial aggregation (Mangan and Wutz 1983). Similarly, the frequencies of predation of *Lygus* by the web-building spiders were much higher in alfalfa (22%) than in strawberries of either treatment (generally 0 to 10%). In this case, spider predation on *Lygus* was almost certainly on nymphs and adults that were caught in spider webs, which are constructed more frequently in areas with high prey concentrations (Harwood et al. 2001, 2003).

Spatial concentrations of *Lygus* in alfalfa trap crops likely increase the localized biological control rendered by natural enemies. As demonstrated by this study and Swezey et al. (2014), both the parasitoid *P. relictus* and generalist predators respond to trap cropping by leveraging higher host/prey densities in alfalfa to increase parasitism and predation, respectively. However, the behaviors associated with specialist and generalist natural enemies that drive pest reductions differ. *P. relictus* specifically targets *Lygus* and therefore has a correlative density-dependent relationship with its host. Polyphagous predators, on the other hand, demonstrate dynamic preferences and responses to prey, often based on relative availability (Symondson et al. 2002). Improvements in *Lygus* predation made by generalists in trap crops are therefore being driven first by exposure to elevated prey densities, and second, by an ability to switch prey sources in response to that increased prey availability (Jaworski et al. 2013). Such switching behavior exhibited by generalists in favor of higher prey densities can be characteristic of type III functional responses between predator and prey (Akre and Johnson 1979).

While trap crops are primarily designed to take advantage of plant host preferences exhibited by a key pest, the subsequent aggregation of that pest nonetheless provides opportunities to enhance natural enemies (Hokkanen 1991, Shelton and Badenes-Perez 2006). This secondary functionality provides a mechanism for conservation biological control that falls outside the more commonly discussed ‘SNAP’ (shelter, nectar, alternate prey, and pollen) modes of action (Landis et al. 2000, Gurr et al. 2017). Characterizing and extending the multiple functions offered by trap cropping (e.g., pest avoidance, targeted management, etc.) continue to be useful in promoting the adoption of this pest management program among growers and pest control advisors.

In summary, The *Lygus* spp. generalist predator arthropod community in organic strawberry was described and evaluated in Monterey County, CA. In total, four different insect taxa and seven different arachnid taxa were found to contain *Lygus* remains. This robust predator assemblage can target this pest from the egg to adult life stages and parallels predator groups found in other *Lygus*-prevalent crops, such as cotton and alfalfa. When predator abundance was compared between alfalfa trap crops and associated strawberry rows, fewer predators than expected responded to the high *Lygus* densities found in alfalfa. Sampling discrepancies regarding where arthropods were collected in differing alfalfa and strawberry canopies may have contributed to these predator abundance equivalencies. Nonetheless, *Lygus* predation frequency found in both insects and web-building spiders was generally higher in trap crops than in strawberry rows. This finding, when combined with previous work documenting improved parasitism in alfalfa trap crops by an introduced specialist parasitoid, illustrates how concentrating prey and host densities in trap crops can conserve biological control agents and broadens the utility of trap cropping in organic strawberry production.

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