

Diversity and phenology of the generalist predator community in apple orchards of Central Washington State (Insecta, Araneae)

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Abstract—Predatory insects and spiders were collected from apple orchards in two geographic regions of Central Washington State, United States of America to assess seasonal phenology and diversity of the generalist predator community. Arthropods were collected from orchard canopy every 3–7 days over two growing seasons (March–October) at seven organically managed and two insecticide-free orchards. Over 35 000 specimens and 80 species of spiders (Araneae), ladybeetles (Coleoptera: Coccinellidae), lacewings (Neuroptera), and predatory true bugs (Hemiptera) were collected. Composition of insect and spider communities differed between the two geographic regions. Indicator species analysis identified several species that had a significant association with one of the two regions. Counts of the most common taxa were examined in detail on a calendar date basis to determine seasonal phenology of adult and immature stages. We observed substantial differences among taxa in number of generations, seasonal timing of first appearance in orchards, overwintering stages, and seasonal occurrence of the adult and immature life stages in orchards. Understanding seasonal phenology of natural enemies in orchards is a core requirement in integrated pest management programs for apple pests, and results of this study provide this information for the generalist predator community of orchards in the Pacific Northwest.

Résumé—Nous avons récolté des insectes prédateurs et des araignées dans des pommeraies dans deux régions géographiques du centre de l'état de Washington, États-Unis d'Amérique, afin d'évaluer la phénologie et la diversité saisonnières de la communauté de prédateurs généralistes. Les arthropodes ont été prélevés dans la canopée du verger à tous les 3–7 jours durant deux saisons de croissance (mars–octobre) dans sept pommeraies soumises à la gestion organique et deux sans insecticides. Les récoltes comprennent plus de 35 000 spécimens et 80 espèces d'araignées (Araneae), de coccinelles (Coleoptera: Coccinellidae), de neuroptères (Neuroptera) et de punaises vraies prédatrices (Hemiptera). Les compositions des communautés d'insectes et d'araignées diffèrent entre les deux régions géographiques. Une analyse des espèces indicatrices identifie plusieurs espèces qui ont une association significative avec l'une des deux régions. Un examen détaillé des dénombrements des taxons les plus communs en fonction des dates du calendrier permet de déterminer la phénologie saisonnière des stades adultes et immatures. Il existe des différences importantes entre les taxons en ce qui a trait au nombre de générations, au calendrier saisonnier de la première apparition dans les pommeraies, aux stades d'hivernage et à la présence saisonnière des stades de vie adultes et immatures dans les pommeraies. La compréhension de la phénologie saisonnière des ennemis naturels dans les pommeraies est une information de base essentielle dans les programmes de lutte intégrée contre les ravageurs des pommes et les résultats de notre étude fournissent ces renseignements pour la communauté de prédateurs généralistes des pommeraies du Nord-Ouest Pacifique.

Introduction

Pest management programs in apple orchards have historically centred on use of insecticides

and miticides to control arthropod pests. Shifts towards less disruptive pest control programs began in the late 1960s with the adoption of control programs that conserve mite predators

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(Hoyt 1969), and continued with the evolution and adoption of mating disruption for managing pest Lepidoptera (summarised in Jones *et al.* 2009). Regulatory changes in the 1990s additionally prompted a shift away from broad-spectrum insecticides to less disruptive products (Jones *et al.* 2009). These changes have created opportunities for growers to move increasingly towards integrated pest management programs that have an emphasis on biological control of pests.

Extensive sampling in orchards has shown that the predatory arthropod community inhabiting the canopy of apple trees is highly diverse (*e.g.*, Chant 1956; Dondale 1956; Oatman *et al.* 1964; McCaffrey and Horsburgh 1980; Carroll and Hoyt 1984; Solomon *et al.* 2000). Capitalising on this potentially important source of pest mortality requires information about the basic natural history of these species, including their seasonal phenology in orchards. Knowledge of seasonal phenology helps predict which specific suite of predators may be present at the appropriate time of year to attack a given pest species. Also, information on phenology is needed to allow growers the option to time insecticide applications in a manner that minimises effects on natural enemies. Although we are seeing a shift by growers from broadly toxic insecticides to selective products, these selective products may nonetheless have disruptive effects on the natural enemy community if applied when susceptible life stages are present (Jones *et al.* 2009).

This study is part of a large, multi-state project to develop new technology (Jones *et al.* 2011) and biological information that can be used by growers to take advantage of natural enemies in fruit and nut orchards. We had two objectives. First, we surveyed apple orchards located in central and southern Washington State to determine taxonomic composition and geographic distribution of predatory arthropods inhabiting the canopy of apple trees. Our survey focused on a large subset of the total predator community, namely the spiders (Araneae), predatory true bugs (Hemiptera: Heteroptera), lacewings (Neuroptera), and ladybeetles (Coleoptera: Coccinellidae), which we know from years of sampling comprise the most common taxa of generalist predators in orchard canopy (Carroll and Hoyt 1984; Miliczky *et al.* 2000; Miliczky and Horton 2005). Second, we determined when, seasonally, adults and the immature stages of

common taxa were present in orchards, to make inferences about generation numbers, seasonal occurrence in orchards, life stages occurring in orchards, and overwintering stage.

Materials and methods

Sites and sampling methods

Canopy-dwelling spiders and predatory insects were collected from four orchards in south-central Washington State and from five orchards in central Washington State, hereafter referred to as the Yakima and Wenatchee sites, respectively (Table 1). Native habitat in the fruit-growing region of Yakima is composed primarily of shrub-steppe plants, dominated by sagebrush (*Artemisia* Linnaeus; Asteraceae) and grasses (Poaceae). The Wenatchee growing region includes more extensive stands of mixed hardwood/coniferous woodland, intermixed with shrub-steppe habitat especially eastwards from Wenatchee. Distances between orchards ranged from 3.5 to 110 km.

Seven of the nine orchards were managed organically, while two orchards received no arthropod controls. The two orchards that received no arthropod controls were treated with antibiotics (for control of fire blight) and herbicides. Six of the nine orchards were sampled in both 2008 and 2009, whereas the remaining three orchards were sampled only in 2008 (Wenatchee Valley College [WVC]) or only in 2009 (QuincyA, QuincyB). Sampling at the WVC orchard was done only in 2008 because the grower shifted from organic management in 2008 to conventional management in 2009; the two Quincy sites were added in 2009 to replace the WVC site (Table 1). At all but two sites, pest control programs during the 2008–2009 study showed no changes from the controls used in the 2 years preceding the study. The only exceptions were at the Wapato site, where Entrust was added to its organic program in 2008 and 2009, and the QuincyB site, which transitioned into organic production in 2008.

Orchard size varied between 0.3 and 11.3 ha (Table 1). Trees were mature (at least 10 years in age) at all locations. Habitats surrounding orchards were generally one of three types: predominantly noncrop vegetation (largely sagebrush-steppe plants); a mix of noncrop and orchard habitats;

Table 1. Location and characteristics of each orchard.

Orchard	Years sampled	Cultivar	Latitude/longitude	Orchard size (ha)	Elevation (m)	% Composition of surrounding habitat (100 m)*			Arthropod pest controls [†]
						Noncrop vegetation	Orchard	Row crop	
Moxee (Y)	2008–09	Red and Golden Delicious	46.495°N, 120.171°W	1.1	477	65	33	0	None
Zillah (Y)	2008–09	Red and Golden Delicious	46.452°N, 120.232°W	11.3	368	10	86	0	MD; O/L.S.; Entrust; Cyd-X
Tieton (Y)	2008–09	Red Delicious	46.740°N, 120.777°W	4.3	647	47	53	0	MD; O/L.S.; Entrust; Cyd-X
Wapato (Y)	2008–09	Golden Delicious	46.481°N, 120.366°W	1.3	323	58	35	0	MD; O/L.S.; Entrust; Cyd-X
TFREC (W)	2008–09	Red Delicious	47.439°N, 120.350°W	0.3	246	15	20	5	None
Sunrise (W)	2008–09	Red Delicious	47.314°N, 120.069°W	6.1	270	32	65	0	MD; O/L.S.; Entrust; Cyd-X; DiPel
WVC (W)	2008	Fuji	47.392°N, 120.202°W	2.5	369	39	56	3	?
QuincyA (W)	2009	Red Chief	47.232°N, 119.968°W	5.3	460	0	89	0	MD, O/L.S.; Cyd-X; DiPel
QuincyB (W)	2009	Superchief Red Delicious	47.203°N, 119.953°W	4.2	432	0	79	10	MD, O/L.S.; Cyd-X; DiPel

*Spatial data derived from orthographic images downloaded from the United States Department of Agriculture Geospatial Gateway (<http://datagateway.nrcs.usda.gov>). A layer of polygons was drawn in ArcMap (ArcGIS 9.2; ESRI, Redlands, California, United States of America) to circumscribe each orchard, using the orthophotographs as background. A 100 m buffer was created surrounding each orchard. A second layer of polygons was drawn to circumscribe the different landscape categories. Areas of each category were totalled for each orchard, with composition for each category then expressed as the proportion of the total surrounding area within the 100 m buffer.

[†] Cyd-X: biological insecticide (virus) directed at codling moth; DiPel: biological insecticide (derived from *Bacillus thuringiensis*) directed at pest Lepidoptera.

(Y), Yakima; (W), Wenatchee; TFREC, Tree Fruit Research and Extension Center; WVC, Wenatchee Valley College; MD, mating disruption; O, oil; L.S., lime sulphur.

or, other orchards. The Tree Fruit Research and Extension Center (TFREC) site is part of the Washington State University-Wenatchee Experiment Station, and is surrounded by laboratories, storage buildings, and other structures. Arthropod pest controls included mating disruption for codling moth (*Cydia pomonella* [Linnaeus]; Lepidoptera: Tortricidae), oil and lime sulphur, Entrust (spinosad), and biological insecticides (DiPel, Cyd-X) for pest Lepidoptera. We note that while spinosad is approved for organic use, the compound may nonetheless harm certain groups of natural enemies (Williams *et al.* 2003). We were unable to obtain spray records for the WVC site, as the orchard was removed from production following the 2009 season.

Canopy-dwelling arthropods were collected every 3–7 days at each orchard beginning in March and extending into September or October. Arthropods were collected by jarring specimens onto beating trays and collecting all specimens into vials for later sorting to species. Samples were taken in the morning as much as possible, when cool temperatures slowed insect movement on trays. Tray sizes were 0.5 m² (Yakima), 0.23 m² (Wenatchee 2008), or 0.10 m² (Wenatchee 2009). Trays were smaller at the Wenatchee sites than the Yakima sites because parasitoids were being collected at the Wenatchee sites as part of another study, and these insects are more easily recovered from small trays than larger trays. Arthropod counts were adjusted to unit tray size for the statistical analyses. We sampled either 50 (Wenatchee) or 30 (Yakima) randomly selected trees at each orchard on each sampling date. One branch was sampled per tree. We selected branches that were 1–2 m above ground, located on the perimeter of the tree canopy. Specimens at the Yakima sites were collected entirely by one person. Specimens from the Wenatchee sites were collected by five to seven people both years. One person (E.R.M.) sorted and identified all specimens. Voucher specimens have been deposited into the M.T. James Entomological Collection at Washington State University (insects) and into the Burke Museum of Natural History and Culture at the University of Washington (spiders).

Arthropods were almost always identified to species. Specimens within certain difficult species complexes (*e.g.*, *Phytocoris* Fallén [Hemiptera: Miridae], larval and female *Hemerobius* Linnaeus

[Neuroptera: Hemerobiidae]) were identified to genus. Identifications were made using several sources of information: our extensive familiarity with the insect and spider faunas in orchards of the Pacific Northwest, published keys, and rearing of immatures. The majority of specimens were identified by relying upon our familiarity with the arthropod fauna in orchards, obtained from over a decade of sampling in Washington State orchards (Horton *et al.* 2001, 2002; Miliczky and Horton 2005, 2007; Miliczky *et al.* 2008). Limited rearing of immature spiders and larval Coccinellidae was done to confirm identifications of less common species or of species within some multi-species complexes. Juvenile spiders in some multi-species genera (*Phidippus* Koch [Salticidae], *Theridion* Walckenaer [Theridiidae]) were occasionally categorised to species on the basis of whether adults of the species were the sole or primary representatives of the genus at the site in question.

Data analysis

Data summaries include primarily graphical presentation of results, with only limited statistical analysis. Statistical analyses were done using the seasonal totals collected at each site for each of the 15 samples (7 sites in 2008 and 8 sites in 2009). Due to differences between the two geographical locations in size of trays and in numbers of trees sampled per orchard (50 versus 30 trees per orchard, in Wenatchee and Yakima, respectively), the counts were standardised to express numbers as totals per unit area of tray (adjusted for sample sizes). Nonmetric multi-dimensional scaling (NMDS) was used to assess similarity of communities among the 15 samples, with the analyses done separately for spiders and insects. The analyses included the combined counts of adult and immature specimens for each taxon except the Coccinellidae; larval Coccinellidae were pooled into a separate, single taxon. For those genera composed of complexes of species not easily separated, we used totals for the genus rather than species totals. Taxa with fewer than 10 specimens summed across all 15 samples were excluded from the analyses. The NMDS ordination was done in PC-ORD (McCune and Mefford 2011) using Sørensen distances. This distance measure is particularly suitable for species community data because it is less affected by zeroes (*i.e.*, species absences) and outliers than other

Table 2. Percentage taxonomic composition of specimens and total number of specimens; pooled adult and immature specimens.

	Yakima		Wenatchee	
	2008 (<i>n</i> = 4 orchards)	2009 (<i>n</i> = 4 orchards)	2008 (<i>n</i> = 3 orchards)	2009 (<i>n</i> = 4 orchards)
Coccinellidae	10.3	16.5	13.7	18.2
Heteroptera				
Anthocoridae	4.2	6.8	0.5	0.7
Miridae	44.2	30.7	39.9	14.3
Other	1.7	1.6	2.5	1.7
Neuroptera				
Chrysopidae	5.7	4.4	5.5	1.9
Hemerobiidae	0.9	1.8	1.1	1.3
Araneae	33.0	38.3	36.9	61.9
Total number of specimens collected	15 614	14 349	2805	2552

Note: Total specimens by orchard shown in parentheses – Moxee 2008 (4108), 2009 (6546); Zillah 2008 (2075), 2009 (1866); Tieton 2008 (4886), 2009 (2801); Wapato 2008 (4545), 2009 (3136); TFREC 2008 (921), 2009 (707); Sunrise 2008 (595), 2009 (433); WVC 2008 (1289); QuincyA 2009 (843); QuincyB 2009 (569).

TFREC, Tree Fruit Research and Extension Center; WVC, Wenatchee Valley College.

distance measures (McCune and Grace 2002; Peck 2010; McCune and Mefford 2011).

Samples were found by NMDS to cluster by geography, so we used indicator species analysis (Dufrene and Legendre 1997) to determine which taxa were commonly associated with one of the two geographic regions. The analysis calculates an index that combines information both on abundance of each taxon in *a priori* defined groups, with presence or absence of taxa among samples or sites within groups. Indicator values vary between 0 (no association with groups) and 100 (perfect association). Statistical significance of an indicator value was tested using a Monte Carlo test. Because our 15 samples (Table 1) were not fully independent (*i.e.*, 6 orchards were sampled both in 2008 and 2009), we eliminated those three orchards that were sampled only in 1 year (retaining the six orchards that were sampled both years), and then blocked the indicator species analysis by year (Peck 2010). The analyses were done using PC-ORD, again following standardisation of the count data to a unit tray area. Analyses were done separately for insects and spiders.

Results

Orchard assemblages

We collected over 35 000 specimens of spiders, predatory true bugs, ladybeetles, and lacewings

from the nine orchards (Table 2). Spiders and predatory Miridae were collected from trays in the highest numbers, followed by ladybeetles and green lacewings (Table 2). Spider numbers increased substantially in 2009 at the Wenatchee sites due to addition of the two Quincy orchards (2009), from which very large numbers of spiders (especially Salticidae) were collected. Totals were substantially higher in the Yakima collections than the Wenatchee collections, in part due to the larger tray used at the Yakima orchards and the larger number of orchards sampled in Yakima (eight in Yakima versus seven in Wenatchee).

Taxonomic diversity was highest for the Araneae and Coccinellidae (Table 3). The spiders included identified representatives from 14 families. The jumping spiders (Salticidae) showed the highest diversity, and were represented by 12 species in eight genera. Theridiidae, Salticidae, and Linyphiidae were numerically the most abundant spiders in collections (Table 4). Coccinellidae included 22 identified taxa distributed among 15 genera (Table 3). The green and brown lacewings (Chrysopidae and Hemerobiidae) both included complexes of congeneric species (*Chrysopa* Leach: three species; *Hemerobius*: four identified species). Seasonal accumulation of new species (*i.e.*, species not collected in any previous month of sampling) showed a sharp increase in May or in April and May for insects and spiders,

Table 3. Genera and species of Coccinellidae, predatory Heteroptera, Neuroptera, and Araneae identified from samples taken at nine apple orchards in Central Washington State, 2008–2009.

Coccinellidae	Araneae
<i>Adalia bipunctata</i> (Linnaeus)	Agelenidae
<i>Anatis rathvoni</i> (LeConte)	<i>Hololena nedra</i> Chamberlin and Ivie
<i>Brumoides septentrionis</i> (Weise)	
<i>Chilocorus stigma</i> (Say)	Anyphaenidae
<i>Coccinella novemnotata</i> Herbst	<i>Anyphaena pacifica</i> (Banks)
<i>Coccinella septempunctata</i> Linnaeus	
<i>Coccinella transversoguttata</i> Faldermann	Araneidae
<i>Cycloneda polita</i> Casey	<i>Araneus gemmoides</i> Chamberlin and Ivie
<i>Harmonia axyridis</i> (Pallas)	<i>Araniella displicata</i> (Hentz)
<i>Hippodamia apicalis</i> Casey	
<i>Hippodamia caseyi</i> Johnson	Clubionidae
<i>Hippodamia convergens</i> Guérin-Méneville	<i>Cheiracanthium mildei</i> Koch
<i>Hippodamia tredecimpunctata</i> (Linnaeus)	<i>Clubiona</i> sp.
<i>Hyperaspidium</i> sp.	
<i>Hyperaspis lateralis</i> Mulsant	Dictynidae
<i>Hyperaspis postica</i> LeConte	<i>Dictyna bostoniensis</i> Emerton
<i>Hyperaspis quadrivittata</i> LeConte	<i>Dictyna coloradensis</i> Chamberlin
<i>Microwisea misella</i> (LeConte)	
<i>Mulsantina picta</i> (Randall)	Gnaphosidae
<i>Psyllobora vigintimaculata</i> (Say)	<i>Sergiolus</i> sp.
<i>Scymnus</i> sp.	
<i>Stethorus punctum</i> (LeConte)	Linyphiidae
	<i>Collinsia ksenia</i> (Crosby and Bishop)
Heteroptera	<i>Erigone</i> sp.
Anthocoridae	<i>Meioneta fillmorana</i> (Chamberlin)
<i>Anthocoris antevolens</i> White	<i>Spirembolus mundus</i> Chamberlin and Ivie
<i>Anthocoris tomentosus</i> Péricart	<i>Walckenaeria subspiralis</i> Millidge
<i>Orius tristicolor</i> (White)	
	Mimetidae
Miridae	<i>Mimetus hesperus</i> Chamberlin
<i>Deraeocoris brevis</i> (Uhler)	
<i>Campylomma verbasci</i> (Meyer-Dür)	Oxyopidae
<i>Phytocoris</i> spp.	<i>Oxyopes scalaris</i> Hentz
Nabidae	Philodromidae
<i>Nabis alternatus</i> Parshley	<i>Apollophanes margareta</i> Lowrie and Gertsch
	<i>Ebo</i> sp.
Geocoridae	<i>Philodromus cespitum</i> (Walckenaer)
<i>Geocoris</i> spp.	<i>Philodromus insperatus</i> Schick
	<i>Philodromus rufus</i> Walckenaer
Pentatomidae	<i>Tibellus</i> sp.
<i>Brochymena quadripustulata</i> (Fabricius)	
Neuroptera	
Chrysopidae	Salticidae
<i>Chrysopa coloradensis</i> Banks	<i>Eris</i> sp.
<i>Chrysopa nigricornis</i> Burmeister	<i>Habronattus</i> sp.
<i>Chrysopa oculata</i> Say	<i>Metaphidippus mannii</i> (Peckham and Peckham)
<i>Chrysoperla plorabunda</i> (Fitch)	<i>Pelegrina aeneola</i> (Curtis)
<i>Eremochrysa</i> sp.	<i>Pelegrina helenae</i> (Banks)
	<i>Phanias watonus</i> (Chamberlin and Ivie)
Hemerobiidae*	<i>Phidippus audax</i> (Hentz)
<i>Hemerobius neadelphus</i> Gurney	<i>Phidippus comatus</i> Peckham and Peckham
<i>Hemerobius ovalis</i> Carpenter	<i>Phidippus johnsoni</i> (Peckham and Peckham)

Table 3. *Continued*

<i>Hemerobius pacificus</i> Banks	<i>Salticus scenicus</i> (Clerck)
<i>Hemerobius stigma</i> Stephens	<i>Sassacus papenhoei</i> Peckham and Peckham
<i>Micromus</i> sp.	<i>Sassacus vitis</i> (Cockerell)
	Tetragnathidae
	<i>Tetragnatha</i> sp.
	Theridiidae
	<i>Enoplognatha ovata</i> (Clerck)
	<i>Theridion murarium</i> Emerton
	<i>Theridion neomexicanum</i> Banks
	<i>Theridion melanurum</i> Hahn
	Thomisidae
	<i>Bassaniana utahensis</i> (Gertsch)
	<i>Misumena vatia</i> (Clerck)
	<i>Misumenops lepidus</i> (Thorell)
	<i>Xysticus cunctator</i> Thorell

Note: Keys or other publications consulted in identifying specimens included: Araneae – Levi (1957), Chamberlin and Gertsch (1958), Dondale and Redner (1978, 1982, 1990), Maddison (1996), Dondale *et al.* (2003), Ubick *et al.* (2005); adult Coccinellidae – Gordon (1985), Acorn (2007); larval Coccinellidae – Rees *et al.* (1994), Rhoades (1996); adult *Chrysopa* – Penny *et al.* (2000); larval Chrysopidae – Flint and Dreistadt (1998); adult Hemerobiidae – Klimaszewski and Kevan (1985).

*Female *Hemerobius* were not identified to species; identifications are for adult males only.

Table 4. Percentage composition of spiders by family for most commonly collected families.

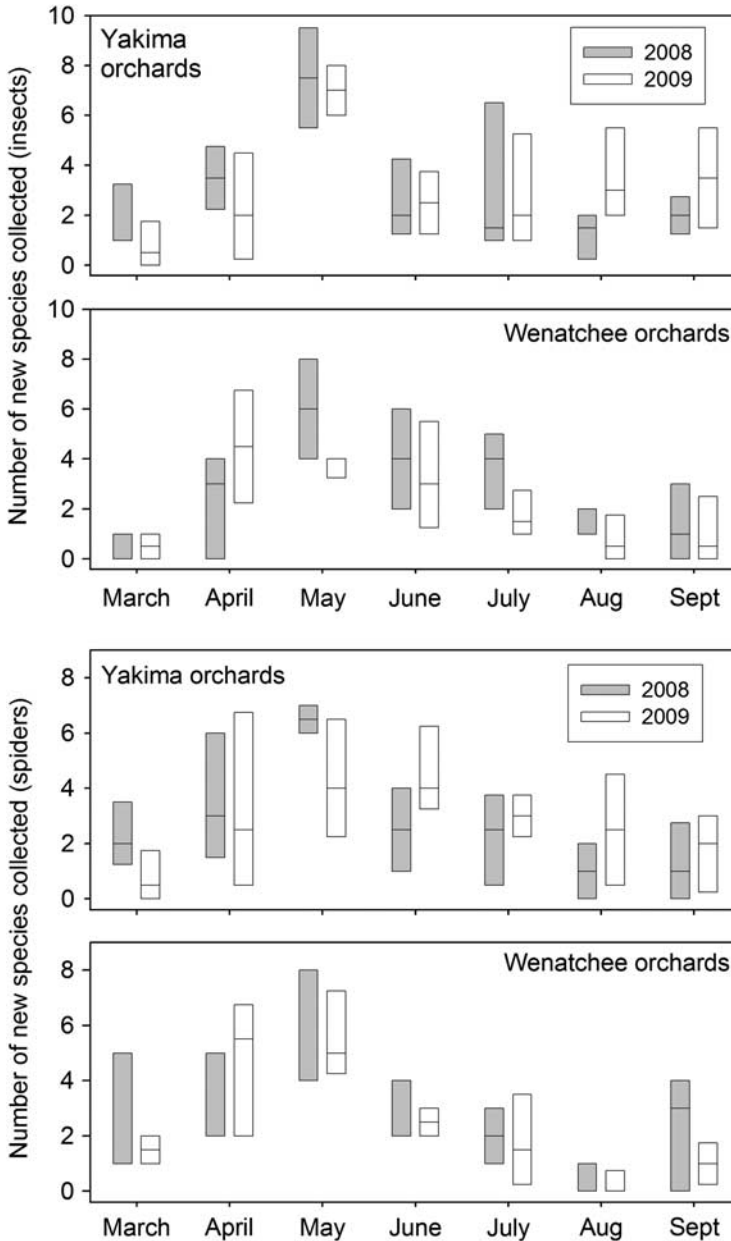
	Yakima 2008	Wenatchee 2008	Yakima 2009	Wenatchee 2009	Overall
Linyphiidae	20.8	12.9	12.1	6.2	14.8
Oxyopidae	7.4	13.6	8.3	11.9	8.8
Philodromidae	3.6	10.1	7.8	4.2	5.9
Salticidae	14.3	22.1	16.5	47.1	19.8
Theridiidae	36.9	23.7	41.8	17.9	35.6
Thomisidae	10.6	6.8	8.4	4.7	8.7

respectively (Fig. 1). Previously uncollected species were found in samples well into September.

Ordination led to clustering of the 15 samples by geography (Wenatchee versus Yakima sites) for both the insects and spiders (Fig. 2); geographic groupings are shown by convex hulls, with centroids of the two groups depicted as stars. Final stress values for the two-dimensional solutions were 11.4 (insects) and 11.3 (spiders). The ordination also showed that pairs of samples collected in consecutive years at the same orchard often clustered together, suggesting that community composition was similar between years at a given site (*e.g.*, note similarity of the insect communities at the Zillah orchard in 2008 and 2009; Fig. 2).

Indicator species analysis using geographic location (Wenatchee versus Yakima) as a grouping factor showed that several species were more common at one location than expected by chance (Table 5). Four taxa (three ladybeetle species and one species of spider) were significantly associated with the Wenatchee location (Table 5). The remaining 10 taxa showing significant association fell into the Yakima group. For some of these taxa, the groupings appeared to be a consequence of total numbers collected within a geographic region, rather than in absence of the taxon from one region. For example, the lacewing *Chrysopa nigricornis* Burmeister was collected from all but one orchard (TFREC 2009), but was substantially more

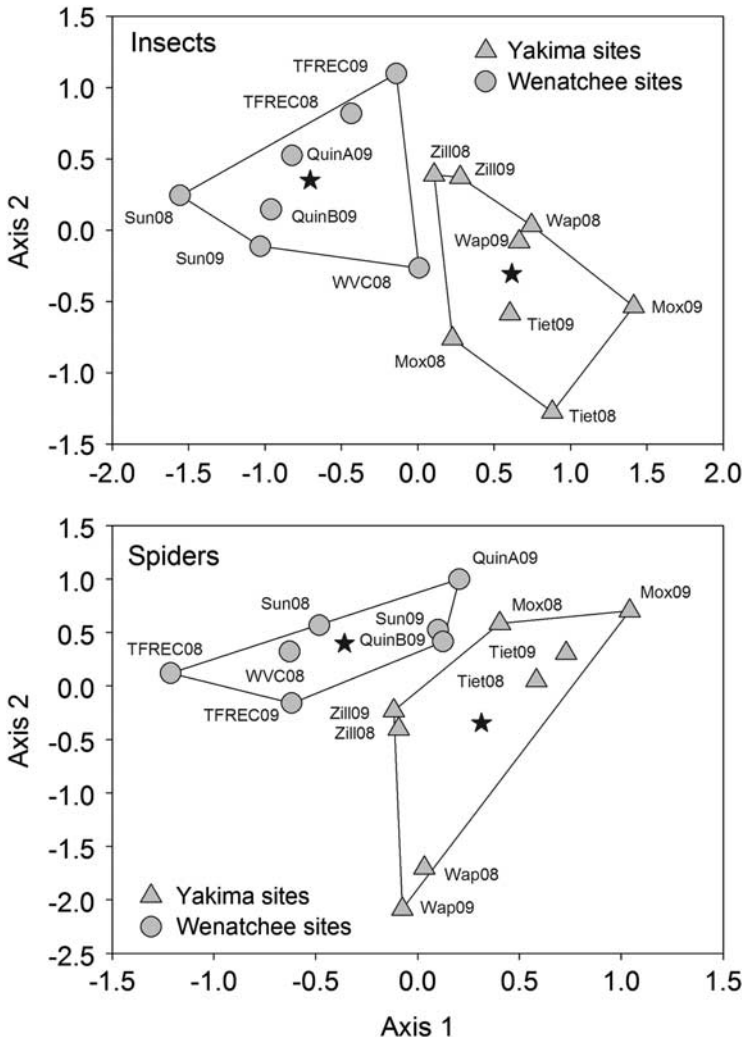
Fig. 1. Box chart showing seasonal distribution in numbers of new species (*i.e.*, those species not collected in any previous month of sampling) for Yakima and Wenatchee orchards. Insects: top two panels; spiders: bottom two panels. Samples sizes (number of orchards) for each box are either three (Wenatchee 2008) or four (all other samples). Each box shows median (horizontal line within box) plus 25th and 75th percentiles.



abundant at the Yakima sites than the Wenatchee sites (counts adjusted to unit tray area). Other taxa, however, did exhibit noticeable geographic effects in presence/absence. Specimens of

Anthocoris Fallén (Anthocoridae) were collected at all Yakima orchards, but were not collected at any Wenatchee orchard. Conversely, *Adalia bipunctata* (Linnaeus) (Coccinellidae) was collected

Fig. 2. Nonmetric multidimensional scaling ordination of the 15 samples in taxonomic space (excludes taxa in which fewer than 10 specimens were collected). Convex hulls show grouping of samples by geographic location (Wenatchee versus Yakima); star symbols show centroids. Counts for three species complexes were included in the ordination at the genus level (*Phytocoris* spp., *Geocoris* spp., *Hemerobius* spp.); larval coccinellids pooled into a single category. Axis 1 and 2 explained 51% and 27% (insects), and 12% and 68% (spiders) of the variation in communities, respectively.



at only one orchard in Yakima (two specimens), but was collected in six of the seven samples from Wenatchee.

Phenology

Seasonal phenology of common taxa is shown as a series of bubble charts (Figs. 3–7). For each taxon in these charts, we selected orchards at which the taxon was collected in the largest numbers. Each horizontal row of bubbles (or

paired rows of bubbles when adult and immature stages are shown together) summarises data for one orchard in 1 year. Within each horizontal row, size of a bubble is proportional to numbers collected on that particular sampling date. Numbers to the right of each chart show total specimens of that taxon and life history stage collected from that particular orchard and year. Vertical dotted lines show mid-point (15th) of each calendar month.

Table 5. List of species showing statistically significant indicator values.

Taxon	Indicator value
Coccinellidae	
(W) <i>Adalia bipunctata</i>	74.4*
(W) <i>Cycloneda polita</i>	82.8*
(W) <i>Psyllobora vigintimaculata</i>	68.4*
(Y) <i>Stethorus punctum</i>	91.7*
Heteroptera	
(Y) <i>Anthocoris</i> spp.	100.0*
(Y) <i>Deraeocoris brevis</i>	90.6**
Neuroptera	
(Y) <i>Chrysopa nigricornis</i>	90.1*
(Y) <i>Chrysoperla plorabunda</i>	83.3*
Araneae	
(W) <i>Theridion murarium</i>	74.7*
(Y) <i>Theridion neomexicanum</i>	90.0*
(Y) <i>Erigone</i> sp.	82.8**
(Y) <i>Tibellus</i> sp.	87.5**
(Y) <i>Meioneta fillmorana</i>	84.1**
(Y) <i>Xysticus cunctator</i>	90.2*

(W) – significant association with the Wenatchee group; (Y) – significant association with the Yakima group. Indicator values vary between 0 (no association) and 100 (complete association).

* $P < 0.05$; ** $P < 0.01$.

Adults of aphidophagous ladybeetles were present in orchards over much of the season beginning in mid-April (Fig. 3). Seasonal phenology of larval aphidophagous ladybeetles is shown for the pooled (taxonomically) sample. Larvae were first collected in mid-May and had virtually disappeared from samples by early July (Fig. 3). The data suggest that the aphid-feeding ladybeetles had but a single larval generation per season in the orchard canopy. The larval sample was composed primarily of specimens of *Coccinella* Linnaeus and *Hippodamia* Dejean (likely to have been mostly or entirely *Hippodamia convergens* Guérin-Méneville, based upon counts of adult *Hippodamia* spp.), with substantially fewer specimens of *Harmonia axyridis* (Pallas), *A. bipunctata* (Linnaeus), *Cycloneda polita* Casey, and *Chilocorus stigma* (Say) (Table 6). Coccinellidae that feed extensively or exclusively on mites or scale insects (*Stethorus punctum* [LeConte], *Microwiseia misella* [LeConte], and *Hyperaspis* Dejean) were most abundant on trays late in the season (Fig. 4).

Common predatory Heteroptera included two species (*Deraeocoris brevis* [Uhler], *Orius tristicolor* [White]) that overwinter in the adult

stage and two taxa (*Campylomma verbasci* [Meyer-Dür], *Phytocoris* spp.) that overwinter in the egg stage (Fig. 5). All four taxa appeared to exhibit two generations of nymphs. Nymphs of the four taxa began to appear in mid-May (Fig. 5).

Brown lacewings (*Hemerobius* spp.) occurred in highest numbers late in the season (Fig. 6). Larval green lacewings were present beginning in mid to late May extending into September. No clear patterns of generations were detected for larval green lacewings (Fig. 6). Adult green lacewings are not effectively sampled using beating trays, and therefore no phenology data are shown for this life history stage. However, our pooled samples for the two most common species (*Chrysoperla plorabunda* [Fitch], *C. nigricornis*) indicated that adults of both species were present most of the season. Adults of *C. plorabunda* were collected seasonally earlier (first seen on trays in March and April) than adults of *C. nigricornis*, which first appeared in orchards beginning in mid-May. Adults of both species were collected in October.

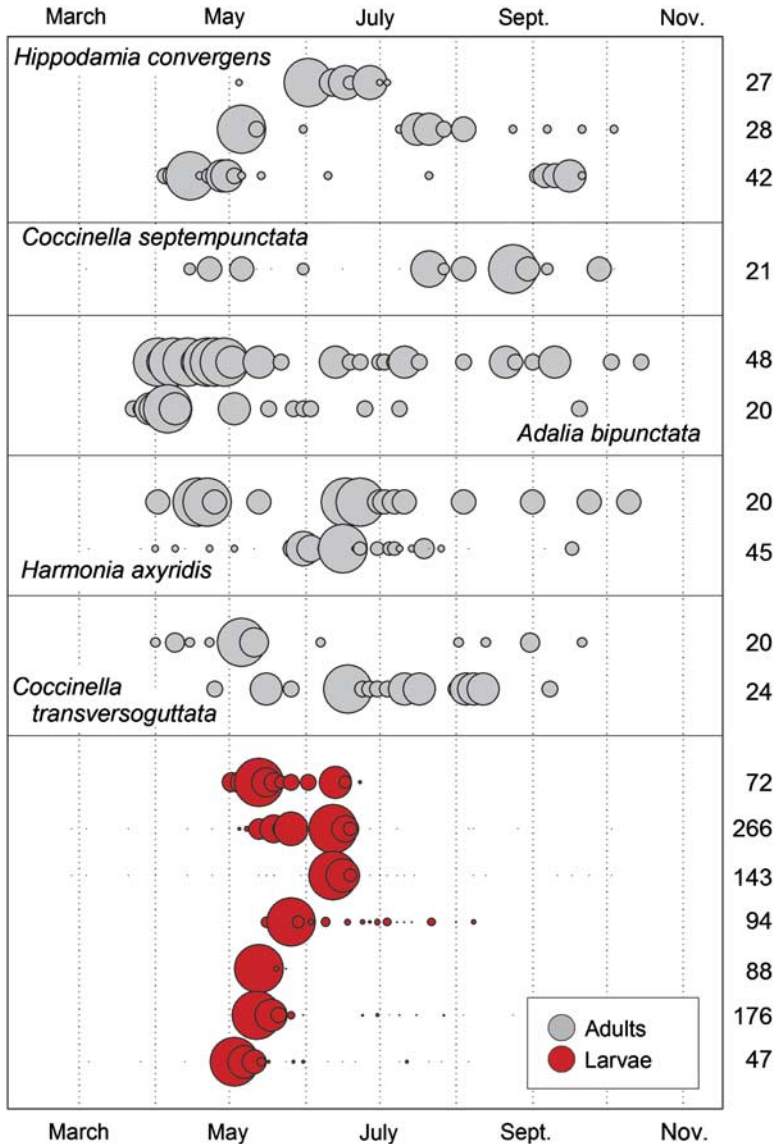
The common taxa of spiders all appeared to have a single generation per year, although species did differ substantially in timing of maturation (Fig. 7). Three general patterns of phenology were observed. First, several species overwintered as juveniles of mixed ages, with adults present generally in mid-summer; examples include *Theridion melanurum* Hahn (Theridiidae), *Philodromus cespitum* (Walckenaer) (Philodromidae), *Sassacus papenhoei* Peckham and Peckham (Salticidae), and *Pelegrina aeneola* (Curtis) (Salticidae) (Fig. 7). At least two species (*Meioneta fillmorana* [Chamberlin] and *Spirembolus mundus* Chamberlin and Ivie [both Linyphiidae]) apparently overwintered as adults or eggs, with juveniles most abundant in mid-summer (Fig. 7). Finally, three species (*Xysticus cunctator* Thorell [Thomisidae], *Oxyopes scalaris* Hentz [Oxyopidae], *Anyphaena pacifica* [Banks] [Anyphaenidae]) were collected only as juveniles, suggesting that mating and egg-laying by these species occurred in habitats other than the tree canopy.

Discussion

Orchard assemblages

The community of predatory arthropods inhabiting the canopy of apple trees in organic or

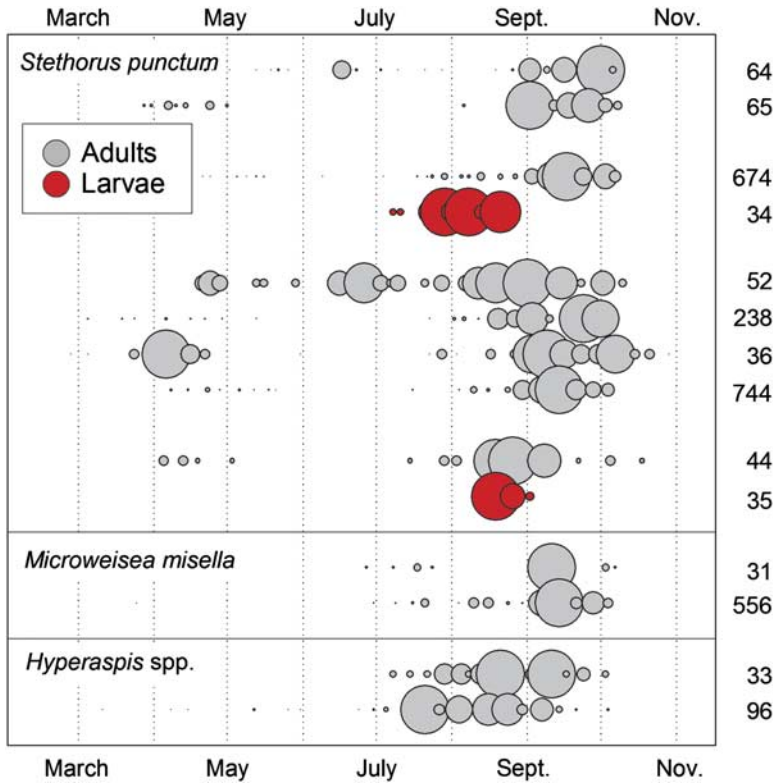
Fig. 3. Bubble chart showing seasonal patterns in numbers of specimens collected: aphidophagous Coccinellidae. Each horizontal row of bubbles shows results for one orchard and 1 year. Within each horizontal row, size of bubble is proportional to numbers of specimens collected on that sampling date. Numbers to right of figure show season-long totals for the taxon collected in that orchard sample. Larval results pool the species. Vertical dotted lines depict the 15th of the month.



unmanaged orchards of Washington State was highly diverse, with over 80 species of Heteroptera, Coccinellidae, Neuroptera, and Araneae identified during 2 years of sampling (Table 3). The relationship between natural enemy diversity and pest suppression is not completely understood. It is not always certain that increases

in diversity of generalist predators necessarily translate into increased suppression of prey (Straub *et al.* 2008; Tylianakis and Romo 2010), because processes such as competition or intra-guild predation may interfere with impact on target pests. Predator diversity is most likely to contribute to increased prey mortality under

Fig. 4. Bubble chart showing seasonal patterns in numbers of specimens collected: other Coccinellidae. Each horizontal row of bubbles or pair of rows shows results for one orchard and 1 year. Within each horizontal row, size of bubble is proportional to numbers of specimens collected on that sampling date. Numbers to right of figure show season-long totals for the taxon collected in that orchard sample. Vertical dotted lines depict the 15th of the month.



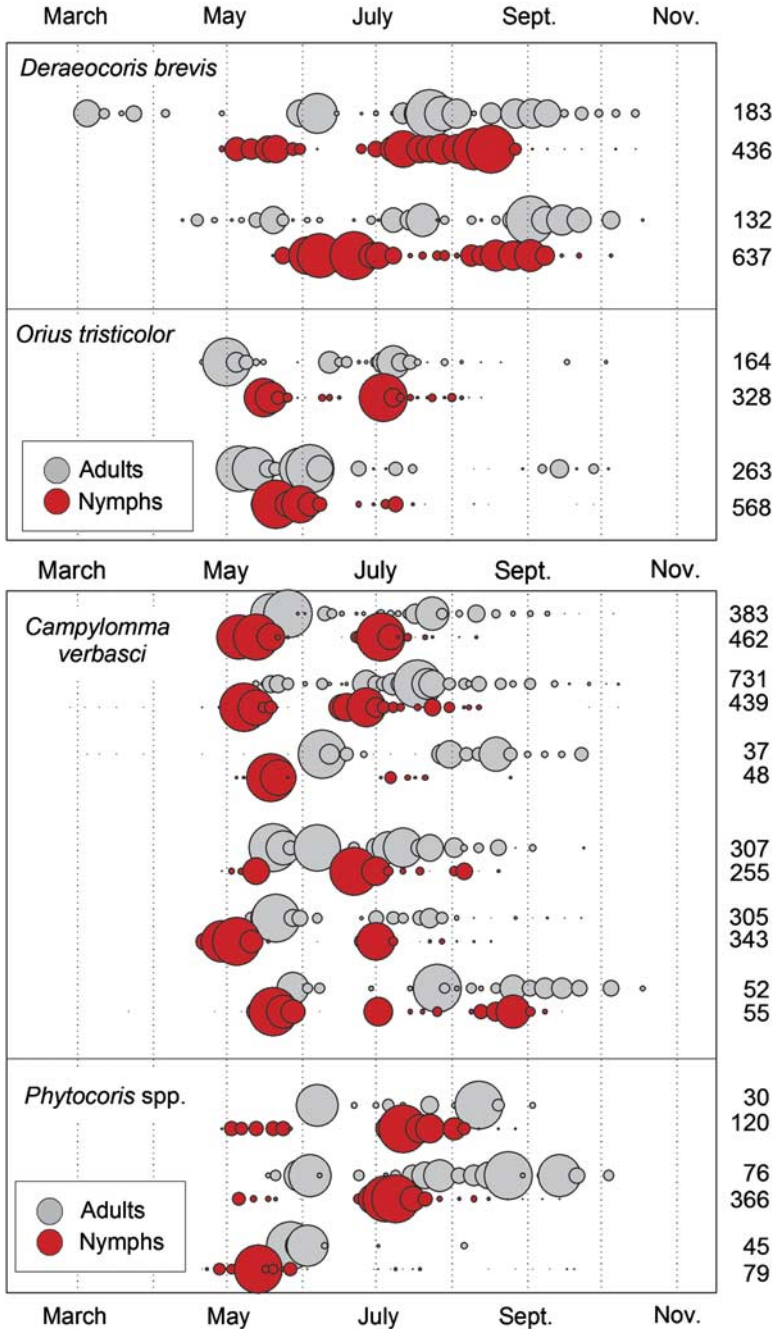
conditions in which natural enemy taxa have complementary effects on pests (Snyder 2009). Such complementarity may be most likely within taxonomic groups in which species exhibit differences in seasonality, prey preferences, or microhabitat use. These very traits may in fact be characteristic of taxonomic groups that are most diverse and most abundant in orchards, such as the Coccinellidae (Snyder 2009) and Araneae (Bogya and Mols 1996).

Our results are in agreement with earlier surveys conducted in apple orchards of North America, which also have documented high diversity of spiders (Dondale 1956; McCaffrey and Horsburgh 1980; Brown *et al.* 2003), true bugs (Oatman *et al.* 1964; Madsen and Madsen 1982), lacewings (Szentkirályi 2001; Horton *et al.* 2002), and lady-beetles (Brown and Schmitt 2001). The taxonomically most diverse groups in this study were the Coccinellidae, with 22 identified species, and

the Araneae, which included representatives from 14 families. Several genera were composed of multiple species (Table 3), including *Hemerobius* with at least four species, *Hippodamia* (four species), and six genera represented each by three species (*Chrysopa*, *Coccinella*, *Hyperaspis*, *Philodromus*, *Phidippus*, *Theridion*). Our results understate the true diversity of predatory arthropods in orchard canopy, because certain taxa are very poorly sampled using beat trays (*e.g.*, adult Chrysopidae, predatory mites). Supplementing results obtained from tray samples with data collected from leaf samples or other monitoring tools (*e.g.*, attractant traps; Jones *et al.* 2011) would provide an even fuller picture of natural enemy diversity in orchards.

The Theridiidae, Salticidae, and Linyphiidae dominated the spider fauna numerically (Table 4). The Salticidae and Theridiidae have been shown to be abundant in apple orchards in other parts of North America and in Europe (Chant 1956;

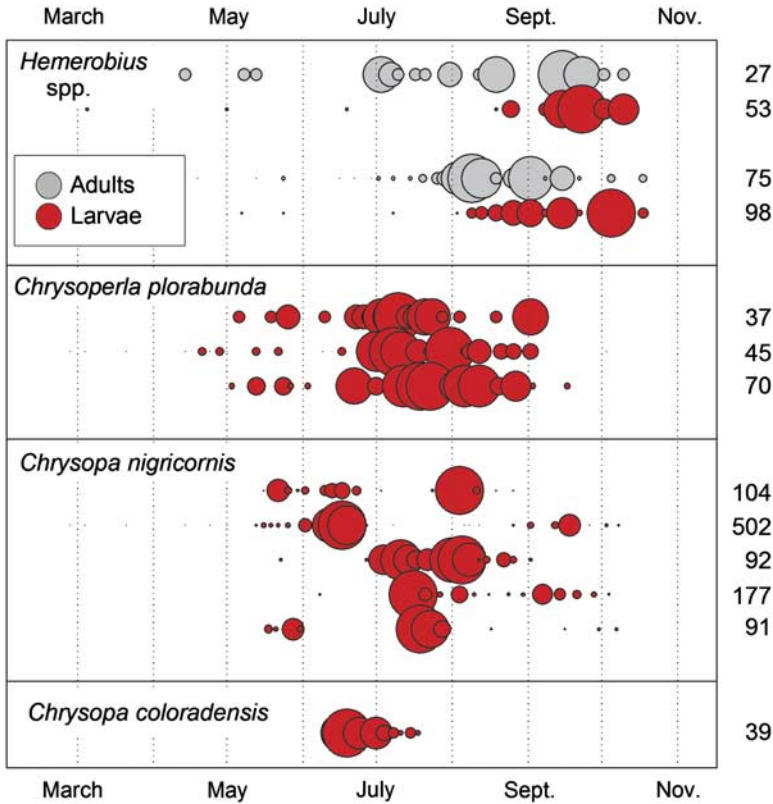
Fig. 5. Bubble chart showing seasonal patterns in numbers of specimens collected: Heteroptera. Each paired horizontal row of bubbles shows results for one orchard and 1 year. Within each horizontal row, size of bubble is proportional to numbers of specimens collected on that sampling date. Numbers to right of figure show season-long totals for the taxon collected in that orchard sample. Vertical dotted lines depict the 15th of the month.



McCaffrey and Horsburgh 1980; Bogya *et al.* 1999; Bajwa and AliNiazee 2001; Brown *et al.* 2003), and may also be among the most common spiders

overwintering in orchards (Horton *et al.* 2001; Miliczky *et al.* 2008). The diet of the spider community in orchard ecosystems is relatively

Fig. 6. Bubble chart showing seasonal patterns in numbers of specimens collected: brown and green lacewings. Each horizontal row of bubbles or pair of rows shows results for one orchard and 1 year. Within each horizontal row, size of bubble is proportional to numbers of specimens collected on that sampling date. Numbers to right of figure show season-long totals for the taxon collected in that orchard sample. Vertical dotted lines depict the 15th of the month.



poorly studied, but is likely to include pests from a range of taxonomic groups (Bogya and Mols 1996). Collections of predatory true bugs included primarily Miridae, as noted also in other geographic regions (Madsen and Madsen 1982; Brown and Schmitt 2001). *Deraeocoris brevis*, which was very abundant in collections, is known to be an important predator of soft-bodied Homoptera such as aphids and psyllids (McMullen and Jong 1967; Unruh *et al.* 2008), while *C. verbasci* (also common in samples) preys extensively on thrips, mites, and Homoptera (McMullen and Jong 1967; Hagley and Allen 1990). Aphidophagous ladybeetles were numerically dominated by species of *Coccinella* and *Hippodamia*, which is consistent with results of other studies (Carroll and Hoyt 1984). We observed noticeable late-season increases at some sites in counts of

Coccinellidae that feed on mites, scale insects, or mealybugs, notably *S. punctum*, *M. misella*, and *Hyperaspis* spp. The most common lacewings were *C. nigricornis* and *C. plorabunda*, both species of known importance in orchards as predators of aphids or other soft-bodied arthropods (Carroll and Hoyt 1984; Szentkirályi 2001).

We observed noticeable geographic effects in composition of spider and insect communities (Fig. 2). Indicator species analysis identified several taxa that occurred more commonly in one geographic region than the other, including taxa that were regularly collected in one location but only rarely collected in the other region. Examples include *A. bipunctata*, which was collected at all but one Wenatchee site, but was very rare in the Yakima collections; and, *Anthocoris* spp., which were not collected from the Wenatchee orchards

Fig. 7. Bubble chart showing seasonal patterns in numbers of specimens collected: spiders. Each horizontal row of bubbles or pair of rows shows results for one orchard and 1 year. Within each horizontal row, size of bubble is proportional to numbers of specimens collected on that sampling date. Numbers to right of figure show season-long totals for the taxon collected in that orchard sample; first number of pair refers to juvenile specimens, while second number refers to adult specimens. Vertical dotted lines depict the 15th of the month.

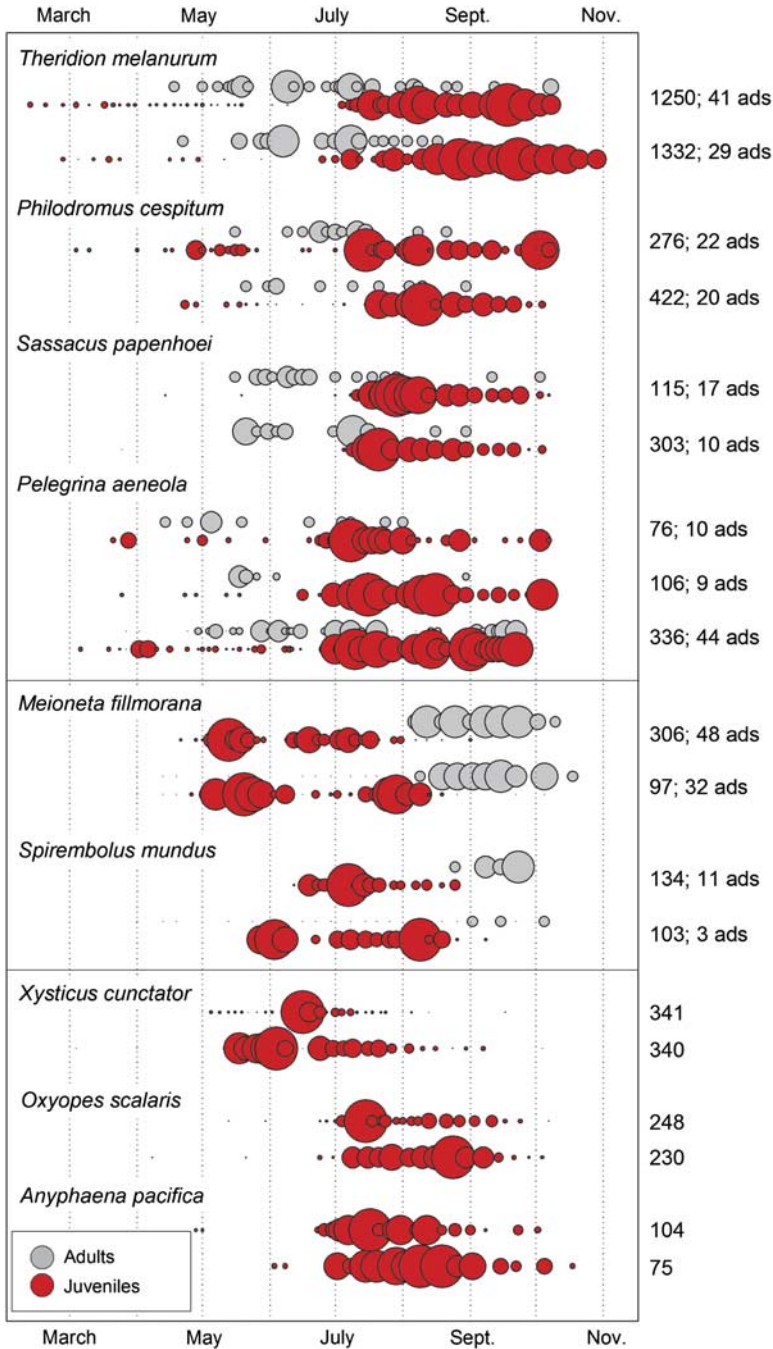


Table 6. Species and genera of larval Coccinellidae collected from Y and W orchards.

Collection period	<i>Hippodamia</i> spp.		<i>Coccinella</i> spp.		<i>Harmonia axyridis</i>		<i>Adalia bipunctata</i>		<i>Cycloneda polita</i>		<i>Chilocorus stigma</i>	
	Y	W	Y	W	Y	W	Y	W	Y	W	Y	W
1–15 May		8		1		1						
16–31 May	145	76	77	22	5	11	1				1	
1–15 June	139	27	65	13	8	1	1	4			1	
16–30 June	101	4	122	1					1	5		
1–15 July	47	9	25	2	3	4	1			2		
16–31 July	2	1	2	1	2	6				2		
1–15 August	1											
16–31 August	1				1							
1 September					1						1	

Numbers show total specimens collected (pooled orchards and years).
Y, Yakima; W, Wenatchee.

but were found relatively consistently in the Yakima samples. The causes of these geographic associations are not known, but could include distribution of preferred prey, landscape effects, or adaptation to local climatic conditions. Geographic effects have been shown to outweigh other factors, including intensity of management practices, in affecting composition of predator communities in apple orchards (Bogya *et al.* 1999; Kondorosy *et al.* 2010).

Our ordinations also showed that communities were often similar between consecutive years at orchards that were sampled both years (Fig. 2). This constancy is not surprising. Taxa common in orchards regularly occur in nonorchard habitats adjacent to orchards (Miliczky and Horton 2005, 2007), thus composition of the orchard community is likely to be affected by neighbouring habitats (which should remain relatively constant between years). Also, insecticide use did not change at any of the orchards between consecutive years. It is of some interest that we observed this year-to-year similarity even at the two orchards in the Wenatchee region that were sampled both years (Sunrise and TFREC orchards; Fig. 2). Given that personnel who did the collecting at these two orchards changed between sample dates and between years, the year-to-year similarity suggests that any variation among people in how effectively or carefully that they collected specimens was largely overshadowed by variation among sites.

We also observed differences in composition of communities among orchards within geographic

location (Fig. 2). Several factors may have contributed to this variation. First, orchards within each geographic location differed in pest control programs (Table 1). Type of insecticides could have affected structure of the predator communities through direct toxicity, or indirectly through effects on the prey community. Pest control programs do affect the composition of spider and predatory insect communities in orchards (Bogya *et al.* 1999; Miliczky *et al.* 2000; Markó *et al.* 2009; Kondorosy *et al.* 2010). Second, it is likely that composition of the phytophagous arthropod community affected structure of each orchard's predator community. For example, we saw late-season influxes of the mite-feeding *S. punctum* at some orchards, which probably is evidence of movement by pest mites into the tree canopy as herbaceous vegetation in and near orchards dried or became senescent. At one orchard (Moxee 2008 and 2009), we also regularly collected ladybeetle species that are known to feed extensively on scale insects (*Hyperaspis* spp., *M. misella*, *Brumoides septentrionis* [Weise], *C. stigma*). This orchard has a history of problems with scale insect pests (D.R.H., personal observation).

Lastly, composition of habitat adjacent to an orchard can affect community structure (*e.g.*, Sackett *et al.* 2008; Markó *et al.* 2009; Kondorosy *et al.* 2010). Orchards differed extensively in type of habitat in immediate proximity (Table 1), and it is possible that this variation partially explains variation among orchards in composition of predator communities. For example, certain sage-loving species such as

Hyperaspis spp. (Rathman and Brunner 1988; Acorn 2007), *Chrysopa coloradensis* Banks (Carroll and Hoyt 1984), or *O. scalaris* (Rathman and Brunner 1988; Miliczky and Horton 2007) were most common at sites (Moxee, Tieton, Wapato) that were adjacent to large areas of sagebrush-steppe habitat (Table 1). It is quite likely that the sagebrush habitats were a source of these sage-loving taxa in our orchard samples.

Phenology

We observed considerable variation among taxa in seasonal phenology (Figs. 3–7). Our summaries depict patterns observed in the tree canopy of apple orchards, and cannot necessarily be extrapolated beyond the orchard canopy to other habitats. Many predatory taxa in orchards are also known to feed and reproduce extensively in habitats outside of orchards (Horton and Lewis 2000; Miliczky and Horton 2005, 2007), and these habitats are likely to compete with orchard habitat as sources of prey, refuge, and overwintering sites. For example, the late-season, single generation shown by some species (*e.g.*, *Hemerobius* spp. or *S. punctum*) was likely caused by late-season movement into the orchard canopy from other habitats, possibly in response to population increases of preferred prey in the orchard. Earlier generations of these predators presumably occurred in habitats other than the orchard canopy. Our phenology data suggest that aphidophagous Coccinellidae produced a single larval generation in orchard canopy (Fig. 3). Voltinism of aphidophagous Coccinellidae may often be affected by availability of prey (Hagen 1962; Hodek 1973), and it is not clear whether the aphid-feeding ladybeetles in these orchards produced additional generations outside of the apple tree canopy. In summary, seasonally abrupt appearances of predatory taxa in orchards, or disappearance of taxa from orchards, may be caused by predator–prey interactions both within and outside of orchards.

How might these phenology data be used in pest control programs? Better understanding of natural enemy phenology is critical to identify intervals in which beneficial taxa would be most vulnerable to applications of insecticides (Jones *et al.* 2009), and in predicting which predators are likely to be active in the orchard when a targeted pest is present. Phenology models are available for a number of arthropod pest species

in Washington orchards (Knight 2007; Jones *et al.* 2010), and growers often use these models in determining appropriate timing for insecticide applications. By knowing phenology of key predators, growers may be presented with additional management options. For example, if important natural enemies of a key apple pest such as codling moth show extensive seasonal overlap with the pest, growers may choose to use highly selective control strategies against the pest (*e.g.*, virus in conjunction with mating disruption) rather than less selective insecticides.

Finally, it would be useful to produce models of phenology that can be used by growers to predict when, seasonally, important taxa are expected to appear in apple orchards. Degree-day models are commonly used to predict seasonal appearances of pest species (Knight 2007). We believe that a similar effort for the generalist predator community in orchards would be more challenging than the development of models for orchard pests. Seasonal appearance of a given predator taxon in orchards is likely to be affected by a number of factors other than accumulated heat units, including densities of prey within the orchard and in neighbouring habitats, and size of the population overwintering within the orchard relative to numbers overwintering outside of orchard habitat (Horton and Lewis 2000). Species that overwinter within orchards as a life history stage that is unlikely to disperse from the orchard upon emergence in spring might most effectively be modelled using degree-day methods. Indeed, such models are available for *C. verbasici* (Judd and McBrien 1994), a species that overwinters in the egg stage, commonly within orchards.

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