

Field Observations on *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) in Oregon

MICHAEL L. LAMANA AND JEFFREY C. MILLER

Department of Entomology, Oregon State University, Corvallis, Oregon 97331-2907

Received April 17, 1995; accepted June 27, 1995

A lady beetle native to Asia, *Harmonia axyridis* Pallas, is established in the Pacific Northwest of North America. Ten years occurred between the intentional release of beetles and the first observation of an individual on July 18, 1991, in Kings County, Washington. The beetle was extremely abundant in western Washington and Oregon throughout 1993-1994, where the species ranged from mideastern Washington, south to just north of the California/Oregon border, east to an elevation of 1371 m in the Cascade Mountains and west to the Pacific Coast. Field sampling confirmed the habits and habitats of *H. axyridis* as a generalist, semiarbooreal, aphidophagous predator. Our records associate *H. axyridis* with 17 aphid prey species on 17 plant hosts. In western Oregon, *H. axyridis* co-occurs with 11 species of native and 2 species of exotic aphidophagous coccinellids on trees and shrubs. In arboreal habitats, 70% of individual lady beetles and 82% of live adult coccinellid mass were represented by *H. axyridis*, while constituting only 4% of the coccinellids in alfalfa, clover, and peppermint. Adult *H. axyridis* dispersed to feeding sites from overwintering aggregations, which formed the preceding October, during March. At least two generations, with a partial to complete third generation, occur per year. Parasitism of field-collected adult beetles by *Dinocampus coccinellae* (Schränk) was less than 1%. © 1996 Academic Press, Inc.

KEY WORDS: Insecta; Coccinellidae; *Harmonia axyridis*; *Dinocampus*; guild; biocontrol; polymorphism.

INTRODUCTION

Recovery of exotic coccinellids in successful classical biological control programs has often been delayed from the time of release (Gordon and Vandenberg, 1991). For example, *Coccinella septempunctata* L. was released in the United States beginning in 1956 before a resident population was discovered in 1973 (Angelet *et al.*, 1979). Similarly, *Hippodamia* (Adonia) *variegata* (Goeze) was released in Canada in the 1950s but not recovered until 1984 in Montreal, Quebec (Gordon, 1987) and 1992 in New York and Vermont (Wheeler,

1993). Both of these species dominated the aphidophagous coccinellid guild in their recovery sites, with *C. septempunctata* and *H. variegata* constituting over 80 and 36% of coccinellids, respectively (Wheeler, 1993; Angelet *et al.*, 1979).

The phenomenon of delayed postrelease recovery accompanied by numerical dominance of the aphidophagous coccinellid guild has been repeated in western Oregon by the multicolored Asian lady beetle *Harmonia axyridis* Pallas. A color-polymorphic, semiarbooreal predator of certain Homoptera/Psocoptera and native to Western Asia (Hukusima and Kamei, 1970), *H. axyridis* was imported to the United States for biological control of pear psylla, pecan aphid, and other arboreal Homoptera. Releases of *H. axyridis* date back to 1916 in California and in many states by the Department of Agriculture between 1978 and 1982 (Chapin and Brou, 1991). Its establishment in North America was first recorded in Louisiana and Mississippi during 1980 (Chapin and Brou, 1991), and then in Georgia by 1990 (Teddners and Schaefer, 1994). Mass releases of *H. axyridis* occurred in three counties of the state of Washington in 1981-1982. A total of 37,852 adult beetles were released in Chelan, Klickitat, and Yakima Counties. Yakima Co. also was the release site of 14,376 larvae in 1978 (Coulson, 1992). On July 18, 1991, an adult was collected in Kings Co., Washington. No known releases of *H. axyridis* were made in Oregon, but it was recorded in Oregon for the first time when one larva was recovered in Kaiser, Marion Co. during October 1991. (R. Westcott, Oregon Department of Agriculture, personal communication). By early spring of 1993 this species was very abundant on aphid-infested trees and shrubs in Corvallis, Benton Co., Oregon (LaMana and Miller, personal observation).

The release of generalist predators for biological control programs has been the subject of debate based on: (1) inconsistent and long delays between release and establishment (e.g., Angelet *et al.*, 1979); (2) possible displacement of other guild members (see Rosenheim *et al.*, 1994); and (3) impacts on nontarget species (Howarth, 1991). The occurrence of *H. axyridis* in

Oregon provided an opportunity to record baseline data on certain aspects of its behavior and ecology during a phase of population expansion into a new environment. The objectives of this study were to: (1) document the occurrence and distribution of *H. axyridis* in Oregon in 1993 and 1994, including different color forms; (2) assess guild composition of semiarboreal, aphidophagous coccinellids between March and October of 1994; (3) document the phenology of all life stages and overwintering; (4) record host plant and prey associations; and (5) document parasitism of larvae, pupae, and adults.

MATERIALS AND METHODS

Distribution and color forms. Field surveys to assess the presence/absence of *H. axyridis* were conducted on September 18, 1993, April 16, 1994, and July 9, 1994. This survey covered approximately 373 km, ranging from Corvallis, Benton Co., south to Ashland, Jackson Co., Oregon 19.3 km north of California. Additionally, surveys of the central region of the Cascade Mountains (Linn, Jefferson, and Deschutes Counties) and Pacific coast areas (Lincoln, Lane, Douglas, Coos, and Curry Counties) were conducted during the springs and summers of 1993 and 1994. A 75 cm \times 75 cm beating sheet was used to collect adult and larval lady beetles from various trees and shrubs. All adult and larval (excluding first instars) aphidophagous coccinellids were identified to species. The occurrence of all color forms of *H. axyridis* (after Komai, 1956) was documented. A proportion of the sampling effort was timed to provide a measure of abundance based on 100 s of sampling effort. Voucher specimens of *H. axyridis* have been placed in the Systematic Entomology Laboratory, Department of Entomology, Oregon State University, Corvallis, Oregon.

Aphidophagous coccinellid guild composition. Shrubs and trees were sampled in September 1993, and then from April 10 to October 30, 1994, using a beating sheet. Individuals representing each coccinellid species were counted and weighed in the laboratory to compare relative abundance and live mass within the guild. All samples for the guild composition analysis occurred in the vicinity of Corvallis. Samples were conducted on windless days in the cool morning or evening hours to minimize flight response by adult beetles. Although sampling was conducted at least twice per month, no individual host plant was sampled twice per 4-week interval. Concurrently, a survey of aphidophagous coccinellids was conducted in fields of alfalfa, clover, and peppermint in the same vicinity. Each of these crops was sampled by conducting 100 180° arc sweeps with a 40.6-cm-diameter net. Six fields (two per crop) were sampled twice per month from June through September of 1993 and 1994. All adult coccinelline and chiloc-

rine lady beetles were identified to species. Larvae were not counted.

Sample data were analyzed to assess community composition of semiarboreal, homopterous coccinellids by month and habitat. The analysis included (Table 1): (1) abundance of each species per sample (ρ , Eq. [1]) and species richness (s , Eq. [2]); (2) a species diversity index ($e^{H'}$, Eq. [5]); (3) a variance estimate for the species diversity index ($\text{var } H'$, Eq. [4]) after Poole (1974); and (4), the Berger-Parker index of dominance (d , Eq. [6]) (Southwood, 1978).

Phenology, prey-species, and parasitism. Phenology of *H. axyridis* was documented in the vicinity of Corvallis each week from April 10 to November 9, 1994. Immature and adult *H. axyridis* were noted by host-plant species and date. Relative abundance of larvae and adults from the field sampling (see above) also was used to assess voltinism. To document prey exploitation patterns, Aphidoidea associated with *H. axyridis* on respective host plants were retained for identification. Incidence of parasitism of *H. axyridis* was determined by maintaining field collected larvae, pupae, and adults in the laboratory. Immatures were reared to adults, and all adults were kept until their death.

RESULTS AND DISCUSSION

Distribution. During approximately 15 months of study, we observed an increase in the range of *H. axyridis* in western Oregon. On September 18, 1993, *H. axyridis* was found from Corvallis south to Myrtle Creek, Douglas Co. (Fig. 1). No *H. axyridis* was col-

TABLE 1

Indices Used to Compare Composition of Aphidophagous Coccinellid Guilds among Months, Habitats, and Plants

Statistic	Equation	Equation number
Sampling abundance (ρ)	$\rho = \frac{n}{\text{sample time}} \times 100$	[1]
Species richness (s)	s , species count	[2]
Shannon-Weaver Index (H')	$H' = - \sum_{i=1}^s \left(\frac{n_i}{n} \ln \frac{n_i}{n} \right)$	[3]
Variance about H'	$\text{var}(H') = \frac{\left(\sum_{i=1}^s p_i \ln^2 p_i \right) - \left(\sum_{i=1}^s p_i \ln p_i \right)^2}{N} + \frac{(s-1)}{2N^2}$	[4]
Species diversity ($N1$)	$N1 = e^{H'}$	[5]
Berger-Parker Dominance Index (d)	$d = n_{\text{dominant}}/n_{\text{total}}$	[6]

lected further south. Similarly, the first survey of the following spring (April 16, 1994) showed no further southerly distribution of *H. axyridis*. However, during the final survey on July 9, 1994, we found *H. axyridis* as far south as Medford, Jackson Co., where one adult and one larva were collected from an ornamental birch (*Betula pendula* L.) (Table 2). In southwestern Oregon, *H. axyridis* was found associated with *Adalia bipunctata* (L.), *Cycloneda polita* Casey, *Olla v-nigrum* (Mulsant), and *C. septempunctata*, but it did not dominate the aphidophagous guild as it did in Benton Co. (see below). In all 1994 collections, the relative abundance of *H. axyridis* decreased south of Benton Co. and was 30.4, 2.2, and 2.3% of adult coccinellids collected in Douglas, Josephine, and Jackson Counties, respectively (Table 2). Thus, by July 9, 1994 *H. axyridis* was found in most western counties of Oregon, indicating its contiguous distribution from Washington state to California. The distribution of *H. axyridis* spanned 1371 m in elevation at the Deschutes Co./Jefferson Co. border just east of the crest of the Cascade Mountains in the east, to sea level in Newport, Lincoln Co. in the west.

Color polymorphism. Three main adult elytral color-forms of *H. axyridis* were recovered in western Oregon. Most of the adults were the morph with orange elytra and black spots (f. *succinea*). A black morph with two red elytral spots (f. *conspicua*) was uncommon in southwestern Oregon, constituting 1.4% ($N = 414$) of *H. axyridis* collected in Lane, Douglas, Jackson, and Josephine Counties. A third, exceedingly rare, black morph with four red elytral spots (f. *spectabilis*) was not found in these southwestern counties, and only one individual out of 2984 was encountered in the intensive sampling in Benton Co. (see below). Thus, relative abundances of these elytral color-forms in western Oregon are extremely dissimilar to those in the southeastern United States, where the melanic forms *con-*

TABLE 2

Locality Records and Relative Abundance of *Harmonia axyridis* Pallas in Western Oregon, 1993–1994

County	Year	Presence		Relative abundance ^a	N ^b
		Larvae	Adults		
Benton	1993	Yes	Yes	N/A ^c	N/A
	1994	Yes	Yes	70.4%	3427
Lane	1993	Yes	Yes	N/A	N/A
	1994	Yes	Yes	58.5%	82
Douglas	1993	Yes	Yes	N/A	N/A
	1994	Yes	Yes	30.4%	112
Josephine	1993	No	No	0.0%	N/A
	1994	No	Yes	2.2%	134
Jackson	1993	No	No	0.0%	N/A
	1994	Yes	Yes	2.3%	86

^a Percent of aphidophagous coccinellids (adults and larvae) comprised by *H. axyridis*.

^b Number of aphidophagous coccinellids in samples.

^c Sampling during 1993 was for presence/absence only.

spicua and *spectabilis* are unknown (Teddars and Schaefer, 1994). In Japan, the source area for cultures released in Washington and the Southeast United States (Coulson, 1991), the forms *conspicua* and *spectabilis* predominate, constituting over 60% of individuals in one study (Komai, 1956). Conversely, in the vicinity of Vladivostok, Russia, melanic forms constituted only ca. 10% of adults (Kholin, 1991).

Aphidophagous coccinellid guild composition. A total of 13 coccinellid species in the subfamilies Coccinellinae and Chilocorinae were collected in Benton Co. In timed arboreal samples, *H. axyridis* accounted for 70.4% of all individuals (adults and larvae) and 82.0% of all adult live mass of coccinellids collected in 14,357 s (Table 3). The four most abundant species were *H. axyridis*, *A. bipunctata*, *C. septempunctata*, and *C. polita*, which accounted for 91.8% of all adults and 96.2% of all adult live mass. These four species constituted 87.3% of all larvae, accounting for 73.8, 3.5, 8.4, and 1.6% of larvae, respectively. The abundance (ρ) of all species differed by month (Table 4). The total number of beetles was highest in May, July, and October, with over 24 beetles per 100 s of sampling time. Beetles were least abundant in June and August when ca. 18.5 beetles per 100 s were collected. Numerical dominance of *H. axyridis* larvae was nearly complete during September and October (Table 4).

In arboreal samples, guild dominance by *H. axyridis* was weaker on conifers ($d = 0.48$) than on angiosperms ($d = 0.73$), as was reflected by the higher species diversity observed on conifers. Although diversity was higher on conifers ($e^{H'} = 3.4$), than on angiosperms ($e^{H'} = 2.9$), absolute coccinellid abundance was much lower on conifers (13.7 beetles/100 s) than on angiosperms (25.9 beetles/100 s). Species diversity differed significantly

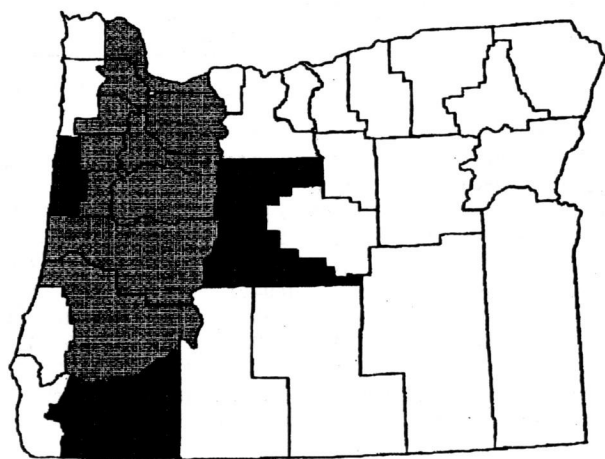


FIG. 1. Recovery of *Harmonia axyridis* in western Oregon counties during 1993 and 1994 (gray) and 1994 only (black).

TABLE 3

Species, Number of Individuals, and Live Mass within the Guild of Aphidophagous Coccinellids in an Arboreal and an Herbaceous Habitat in Benton Co., Oregon, (April–October 1994)

Species	Habitat ^a	n	Adults		n	%
			% Individuals	% Mass		% Individuals
<i>Harmonia axyridis</i>	A	2079	69.6	81.6	333	75.2
	B ^b	29	3.7	5.5		
<i>Adalia bipunctata</i>	A	396	13.3	6.3	15	4.5
	B	4	0.5	0.3		
<i>Coccinella septempunctata</i>	A	149	5.0	7.0	4	0.9
	B	214	27.4	47.7		
<i>Cycloneda polita</i>	A	116	3.9	1.4	37	8.4
	B	11	1.4	0.6		
<i>Exochomus quadripustulatus</i> (L.)	A	110	3.7	1.4	25	5.6
	B	0	0.0	0.0		
<i>Mulsantina picta</i> (Randal)	A	35	1.2	0.3	16	3.6
	B	3	0.4	0.1		
<i>Calvia quatuordecimguttata</i>	A	17	0.6	0.4	9	2.0
	B	0	0.0	0.0		
<i>Coccinella trifasciata</i>	A	25	0.8	0.4	3	0.7
	B	376	48.2	31.6		
<i>Hippodamia sinuata</i> Mulsant	A	29	1.0	0.5	0	0.0
	B	55	7.4	4.1		
<i>Hippodamia convergens</i>	A	18	0.6	0.4	1	0.2
	B	73	9.4	8.2		
<i>Coccinella californica</i> Mannerheim	A	6	0.2	0.2	0	0.0
	B	14	1.8	1.8		
<i>Myzia subvittata</i> (Mulsant)	A	2	0.1	0.1	0	0.0
	B	0	0.0	0.0		
<i>Chilocorus</i> sp.	A	2	0.1	0.0	0	0.0
	B	0	0.0	0.0		
<i>Coccinella undecimpunctata</i> L.	A	0	0.0	0.0	0	0.0
	B	1	3.6	0.01		
Totals	A	2984			443	
	B	780			N/A	

^a A, trees and shrubs; B, clover, alfalfa, and peppermint.

^b Larvae were not sampled in the herbaceous habitat.

by month and was moderate in April, May, and August, highest in June and July, and very low in September and October because of the near complete dominance of *H. axyridis* (Table 4). Although the arboreal coccinellid guild was dominated by *H. axyridis* each month, the dominance ranged from 49.8% of all coccinellids in June to 96.3% in October. Abundance of adult *H. axyridis* was relatively constant, ranging from 12.8 to 19.8 beetles per 100 s, for all months except May when only 6.8 *H. axyridis* per 100 s were observed.

Twelve species of Coccinellidae were observed in sweep-net sampling in alfalfa, clover, and peppermint. In contrast to its predominance in arboreal samples, *H. axyridis* was a minor guild component in these herbaceous crops, constituting only 3.7% of adult coccinellids ($N = 780$) and 5.5% of adult mass (Table 3). The four most abundant coccinellids in these three crops were *Coccinella trifasciata* LeConte, *C. septempunctata*, *Hippodamia convergens* Guerin, and *Hippodamia sinuata* Mulsant, which accounted for 48.2, 27.4, 9.4, and 7.4% of adults, respectively. In contrast to the numerical domination of the arboreal guild by *H. axyridis*, the alfalfa, peppermint, and clover systems were dominated each month by *C. trifasciata* ($d = 0.32$ to 0.68), except during June and July when the aphidophagous coccinellid guild in these three crops was codominated by *C. trifasciata* and *C. septempunctata*. Because of different sampling methods, a comparison of the absolute abundance of *H. axyridis* in trees/shrubs versus the herbaceous plants was not possible, but species diversity ($e^H \pm SE$) of coccinellids was significantly higher in herbaceous habitats ($e^H = 4.7 \pm 0.3$) than in arboreal habitats ($e^H = 3.1 \pm 0.1$) (see Table 5).

Phenology. In Benton Co., adult *H. axyridis* dispersed from overwintering aggregations in March 1994, and accounted for 76% of coccinellid adults in timed samples during the first two weeks of April. Copulation was documented on March 27 and sporadically through the season and last recorded on October 5. Oviposition by *H. axyridis* was observed from April 7 to October 1994. Larvae were first detected on May 9, when *H. axyridis*, *A. bipunctata*, and *Calvia quatuordecimguttata* L. were collected simultaneously. Abundance of *H.*

TABLE 4

Indices Describing Various Attributes of the Arboreal Coccinellid Guild by Month (Benton Co., Oregon, April–October, 1994)

Month	n	s	p	d ^b	e ^H	Index ^a
						95% C.I. for e ^H
April	304	9	29.4	0.674	3.1ac	2.70–3.55
May	196	8	24.0	0.735	2.5a	2.14–2.98
June	420	8	18.6	0.498	4.2b	3.83–4.50
July	1052	10	33.4	0.557	4.0bc	3.42–4.75
August	722	11	18.5	0.787	2.5a	2.30–2.79
September	148	8	19.7	0.944	1.3d	1.24–1.45
October	484	8	24.9	0.963	1.2d	1.14–1.35
Total	3426	13	23.9	0.704	3.1	2.95–3.22

^a s, Species richness; p, sample abundance; d, dominance; e^H, species diversity; and n, all adults and larvae in samples in given month.

^b Dominant species was *H. axyridis* in each month.

^c Estimates in a column followed by the same letter are not significantly different ($\alpha = 0.05$).

axyridis larvae was high in May and June, averaging 6.5 and 5.9 larvae/100 s, respectively; they then decreased to a low of 0.6 larvae/100 s in August. Larval abundance increased to 6.1 larvae/100 s in October. The abundance of larvae in late fall was particularly notable because no other species was present as larvae after August (see Table 4).

The bimodality in larval abundance suggests bivoltinism, but we observed what appears to have been a third generation in 1993 and 1994. Pupae and larvae were observed in the field as late as November 11. These late pupae were quite often small and dark, indicating larvae had been exposed to a low temperature. Small pupae were coincident with low prey density during "leaf-fall." *Harmonia axyridis* is reportedly multivoltine in Japan.

Aggregations of *H. axyridis* were first observed in late October during 1993 and 1994. Adult *H. axyridis* were observed aggregating on buildings and natural edifices that were prominent, exposed and, often, light in color. All color-forms, *succinea*, *spectabilis*, and *conspicua*, were observed aggregating together. Some beetles of the orange *succinea* morph were very light, a condition that often indicates recent adult emergence (LaMana and Miller, personal observation), and supports the hypothesis that the ultimate generation proceeds directly to overwintering sites. No other species of coccinellid was observed in these aggregations.

TABLE 5

Indices Describing Various Attributes of the Arboreal Coccinellid Guild by Host Plant (Benton Co., Oregon, April–October, 1994)

Plant	Index ^a				
	Time (s)	n	s	p	e ^{H'}
<i>Acer platanoides</i> L.	803	111	6	13.8	2.4
<i>Acer saccharum</i> Marsh	638	49	5	7.6	2.9
<i>Betula pendula</i> L.	2579	664	9	25.7	2.2
<i>Humulus lupulus</i> L.	462	119	9	25.8	4.5
<i>Juglans nigra</i> L.	296	84	8	28.4	4.4
<i>Liriodendron tulipifera</i> L.	2307	977	10	42.5	2.2
<i>Picea sitchensis</i> (Bong.) Carr.	136	32	4	23.5	3.3
<i>Pinus contorta</i> Dougl.	195	15	3	7.7	1.6
<i>Pinus mugo</i> L.	383	116	7	30.3	3.1
<i>Pinus sylvestris</i> L.	465	35	6	7.5	4.0
<i>Prunus persica</i> Batsch.	243	75	6	30.9	3.7
<i>Prunus</i> sp.	139	31	4	22.3	3.3
<i>Pseudotsuga menziesii</i> (Mirb.) Fra.	573	83	7	14.5	4.0
<i>Quercus garryana</i> Dougl. ex Hook.	95	15	4	15.8	2.0
<i>Quercus palustris</i> Muench.	258	19	4	7.4	2.8
<i>Quercus rubra</i> L.	905	221	6	24.4	2.2
<i>Tilia americana</i> L.	1133	383	8	33.8	2.5
<i>Ulmus americana</i> L.	841	210	9	25.0	2.2

^a n, number of larvae and adults; s, species richness; p, sample abundance; e^{H'}, species diversity.

TABLE 6

Host Plant and Prey Records for *Harmonia axyridis* in Benton Co., Oregon, 1993–1994

Host plant	Prey/food	<i>H. axyridis</i> Life stage ^a
<i>Abies procera</i> Rehder	<i>Cinara</i> sp.	L, A
<i>Acer saccharum</i> Marsh	<i>Periphyllus testudinaceae</i> (Fernie)	A
	<i>Drepanaphis idahoensis</i> Smith & Dilley	E, L, P, A
<i>A. saccharum</i>	<i>Drepanosiphum platanoides</i> (Schränk)	E, L, P, A
<i>A. saccharum</i>	<i>Eucera aphid betulae</i> (Kalterbach)	E, L, P, A
<i>Betula pendula</i> Roth	<i>Callipterinella calipterus</i> (Hartig)	L, P, A
<i>B. pendula</i>		
<i>Cirsium arvense</i> (L.) Scop.	<i>Aphis fabae</i> Scopoli	L, A
<i>Dipsacus sylvestris</i> Huds.	<i>Macrosiphum rosae</i> (L.)	L, A
<i>Fagus sylvatica</i> L.	<i>Phyllaphis fagi</i> (L.)	P, A
<i>Humulus lupulus</i> L.	<i>Phorodon humuli</i> (Schränk)	L, P, A
	<i>Illinoia liriodendri</i> Monell	E, L, P, A
<i>Liriodendron tulipifera</i> L.	<i>Acyrtosiphon pisum</i> (Harris)	A
<i>Medicago sativa</i> L.	<i>Ovatus crataegarius</i> (Walker)	A
<i>Mentha piperita</i>	<i>Aphis fabae</i> Scopoli	E, L, P, A
<i>Nasturtium</i> sp.	<i>Hyalopterus pruni</i> (Geoffrey)	A
<i>Prunus</i> sp. (Plum)	<i>Myzocallus occultus</i> Richards	L, P, A
<i>Quercus rubra</i> L.	<i>Macrosiphum rosae</i> (L.)	L, A
<i>Rosa</i> sp. (Ornamental)	<i>Tuberolachnus salignus</i> (Gmelin)	A
<i>Salix</i> sp. (Exotic)	Pollen and nectar	L, P, A
<i>Spirea douglasii</i> Hook.	<i>Eucalyptus tiliae</i> (L.)	E, L, P, A
<i>Tilia americana</i> L.		

^a E, egg, L, larva, P, pupa, A, adult.

Prey species. Seventeen species of aphids were identified as prey for *H. axyridis* on 17 host-plant species (Table 6). Adult and immatures beetles co-occurred in all but four host species, including alfalfa and peppermint, confirming the habits of *H. axyridis* as a polyphagous, arboreal predator. The apparent ability of *H. axyridis* to complete development on the black bean aphid (*Aphis fabae* Scopoli) is interesting in that many species cannot develop on, and usually will not eat, this aphid (Hodek, 1973).

Parasitism. A braconid, *Dinocampus coccinellae* (Schränk), was the only parasitoid reared from *H. axyridis* in Oregon. The rate of parasitism was low, less than 1%. Only two *D. coccinellae* were observed from over 2000 wild adult and larval beetles held in mass cultures in the laboratory. The wasps were reared from two field-collected adults collected in Benton Co. No parasites were reared from beetles collected as immatures.

The dominance of the guild of arboreal, aphidophagous coccinellids in western Oregon by *H. axyridis* is remarkable in both rate of geographic spread and the magnitude of the resulting population. The low rate of parasitism, bivoltinism, and large size all may have contributed the dominance of the arboreal niche by *H. axyridis*. The range of *H. axyridis* is still increasing to the south in the Pacific Northwest, and relative abundances of arboreal coccinellids likely are in flux. Because of the fortuitous spread of this species into Oregon, biological control of arboreal aphids, e.g., filbert aphid and pests of urban shade trees such as tulip poplar, linden, and European birch, is likely to be improved.

ACKNOWLEDGMENTS

We thank J. E. Miller for tireless field work, A. S. Jensen for identifications of Homoptera, and P. M. Mindas-LaMana for invaluable field and laboratory assistance. This research was funded in part by USDA Special Grant Program 93-34205-8437. This is Oregon State University Experiment Station Technical paper No. 10901.

REFERENCES

- Angelet, G. W., Tropp, J. M., and Eggert, A. N. 1979. *Coccinella septempunctata* in the United States: Recolonizations and notes on its ecology. *Environ. Entomol.* **8**, 896-901.
- Chapin, J. B., and Brou, V. A. 1991. *Harmonia axyridis* Pallas, the third species of the genus to be found in the United States. *Proc. Entomol. Soc. Wash.* **93**, 630-635.
- Coulson, J. R. 1992. Releases of Beneficial Organisms in the United States and Territories—1982, p. 207. U. S. Department of Agriculture, Miscellaneous Publication No. 1505.
- Gordon, R. D. 1987. The first North American records of *Hippodamia variegata* (Goeze) (Coleoptera: Coccinellidae). *J. NY Entomol. Soc.* **95**, 307-309.
- Gordon, R. D., and Vandenberg, N. 1991. Field guide to recently introduced species of Coccinellidae (Coleoptera) in North America, with a revised key to North American genera. *Proc. Entomol. Soc. Wash.* **93**, 845-864.
- Howarth, F. G. 1991. Environmental impacts of classical biological control. *Annu. Rev. Entomol.* **36**, 485-509.
- Hukusima, S., and Kamei, M. 1970. Effects of various species of aphids as food on development, fecundity and longevity of *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae). *Res. Bull. Fac. Agric. Gifu Univ.* **29**, 53-66.
- Kholin, S. K. 1991. Stability of genetic polymorphism for wing sheath coloring in *Harmonia axyridis* Pallas (Coccinellidae, Coleoptera) in the Primor'e Region. *Sov. Genet.* **26**, 1449-1454.
- Komai, T. 1956. Genetics of ladybeetles. *Adv. Genet.* **8**, 155-188.
- Ludwig, J. A., and Reynolds, J. F. 1988. "Statistical Ecology," p. 71-95. Wiley, New York.
- Poole, R. W. 1974. "An Introduction to Quantitative Ecology." McGraw-Hill, New York.
- Rosenheim, J. A., Wilhoit, L. R., and Armer, C. A. 1994. Influence of intraguild predation among generalist insect predators on the suppression of an herbivore population. *Oecologia* **96**, 439-449.
- Southwood, T. R. E. 1978. "Ecological Methods," p. 427. Chapman & Hall, London.
- Tedders, W. L., and Schaefer, P. W. 1994. Release and establishment of *Harmonia axyridis* (Coleoptera: Coccinellidae) in the southeastern United States. *Entomol. News* **105**, 228-243.
- Wheeler, A. G., Jr. 1993. Establishment of *Hippodamia variegata* and new records of *Propylea quatuordecimpunctata* (Coleoptera: Coccinellidae) in the eastern United States. *Entomol. News.* **104**, 102-110.