THE KNOWN DISTRIBUTION OF THE PREDATOR *PROPYLEA QUATUORDECIMPUNCTATA* (COLEOPTERA: COCCINELLIDAE) IN THE UNITED STATES, AND THOUGHTS ON THE ORIGIN OF THIS SPECIES AND FIVE OTHER EXOTIC LADY BEETLES IN EASTERN NORTH AMERICA[1]

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ABSTRACT: We provide 86 new collection records for the exotic *P. quatuordecimpunctata,* increasing its known range from 13 to 99 counties, and from three to nine states. The recovery data indicate that the actual distribution of this coccinellid is likely even larger, because systematic and broad surveys have been done in only a few areas. Evidence provided for *P. 14-punctata* and five other aphidophagous coccinellids [*Coccinella undecimpunctata, C. septempunctata, Harmonia axyridis, H. quadripunctata,* and *Hippodamia variegata*] indicates that all six species were first established accidentally in eastern North America, and that they most likely were introduced through seaports. Inland ports appear to facilitate establishment, compared to urban, coastal ports.

Lady beetles have long been recognized as one of the most important groups that prey on insect pests, especially on aphids and other Homoptera. Following the spectacular success of the Vedalia beetle in controlling the cottony-cushion scale in California citrus in the late 1880s (DeBach 1964), numerous attempts to establish foreign aphidophagous coccinellids have been made in the eastern United States, especially during the past 30 years (e.g. Shands *et al.* 1972, Angalet *et al.* 1979). However, nearly all of these intentional releases have failed to persist, and it is an interesting paradox that six aphidophagous coccinellid species have accidentally established themselves during this same period.

Propylea quatuordecimpunctata (L.). is one of the six species of exotic aphidophagous coccinellids discovered to be established in eastern North America since 1912. This paper documents its dispersion southward, as demonstrated by new state and new county collection records.

In addition, we discuss the probable means of entry into North America of *P. quatuordecimpunctata* (*P. 14-punctata* hereafter) and five other lady beetles, and briefly reflect on the significance of the apparent displacement of several native coccinellids by some of the exotic lady beetles.

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MATERIALS AND METHODS

Records for the initial collection of each of the six coccinellid species were obtained from the literature, USDA-APHIS files (Niles, MI; D.R.P. & D.J. Nelson), CAPS (Cooperative Agricultural Pest Survey) data files (Storrs, CT; D.R.E. & R.G. Adams), and from field collections (W.H.D., R.J.C. & staff). We cite the earliest collection date for each species and county because it is most useful for dispersion studies; in a few cases, these precede dates published previously.

Most of the collections of *P. 14-punctata* and other coccinellids were made by sweeping low foliage with an insect net, but several other methods were used, and these are listed with the corresponding records. To prevent escape of any coccinellids, each sweep-net sample by W.H.D. was placed inside a glass-topped sleeve cage before the contents were sorted and counted.

In both Canada and the United States, federal quarantine regulations require issuance of a permit prior to the release of foreign beneficial insects from a quarantine facility. These records were checked to determine if an establishment at each location was preceded by one or more intentional releases in the vicinity.

RESULTS AND DISCUSSION

Propylea 14-punctata: This species was first detected in North America in 1968, near Quebec City, Quebec, by Chantal (1972). Quarantine records in Canada (M. Sarazin, pers. commun.) and the United States (L. R. Ertle, pers. commun.) indicate that no releases of this foreign predator had been made in Canada or the northeastern U.S. prior to this discovery. As Dysart (1988) noted, the evidence clearly indicated that this coccinellid had been present for several years in Quebec before it was first collected. Thus it was not surprising that by 1986, *P. 14-punctata* had been found in 14 counties in Quebec, and had moved southward into three counties in northern Vermont and New York (Dysart 1988).

Table 1 contains the known distribution of this species in the U. S., compiled from our records, data of cooperators, and the literature. Most of these records have not been published – six of the nine state listings are new, as are 86 of the 99 county records. Voucher specimens for records published here for the first time are located at Niles, MI, Newark, DE, and Trenton, NJ.

Based on the dates and locations of many of these first collections on the map (Figure 1), it is obvious that the distribution pattern of *P. 14-punctata* in the U.S. is an extension of the initial establishment in Quebec, and that its dispersion southward is considerable (1,120 km/700 mi.). In addition, if these data are compared to Table 1 using a map with labeled counties, adjacent counties will be found to have different first collection dates. This pattern and the small number of (and widely-spaced) initial positive recovery counties

usually indicate the lack of broad and contemporaneous surveys, rather than absence of the coccinellid, because multi-county surveys later (Table 1) usually detected this species in many additional counties. For example, the 1992 survey results (Table 1: Dutchess, Putnam, & Renssalaer Counties in New York, and Hunterdon, Mercer, & Sussex Counties in New Jersey) suggest that thorough surveys would find *P. 14-punctata* in additional counties west of the Hudson River in New York, and in the eastern border counties of Pennsylvania – and field work in 1993 did detect this beetle in four new counties in western New York (Fig. 1) and in eight counties in eastern Pennsylvania (Table 1).

Other adventive coccinellids: Five species of exotic, predaceous coccinellids have become established over large areas of eastern North America since 1912, as has *P. 14-punctata.* These are listed in Table 2, along with pertinent data, and sources of this information.

Origins of introduced species: The initial distribution of each of the six adventive species of lady beetles was so limited (Schaeffer 1912, Wheeler & Hoebeke 1981, Vandenberg 1990, Dysart 1988, Angalet *et al.* 1979, Gordon 1987, Chapin & Brou 1991) that we can be reasonably certain that they had been present there for a relatively short time. Each species was first found close to a seaport or a shipping lane (identified in Table 2), and five of these seven cases had never been released in that region (details are in footnotes, Table 2). In each of the other two cases (*H. axyridis* in Louisiana and *C. 7-punctata* in New Jersey), the initial recovery locations were distant from the places where the limited prior releases had been made, and these coccinellids were not detected at their release locations within 10 years (footnotes, Table 2). Thus we agree with Schaefer & Dysart 1988[6] that "... circumstantial evidence ... suggests that accidental arrivals on ships is very probable ..." To this we would add that although aircraft would appear to favor insect introductions by virtue of their short transit times, they are inferior to ships for the following reasons: 1) aircraft are much smaller, and have fewer exterior hiding places that are accessible to large numbers of beetles (chances of successful establishment increase as the number of individual immigrants increases); 2) spaces outside the passenger and cargo compartments are not heated [air temperatures at cruising altitude (10,000 m) are – 35° C (calculations from Finch & Trewartha 1949)]; 3) shipments of plant material in cargo are inspected by quarantine personnel; 4) the usual "in port" time of aircraft (hours) is short compared to ships (days) and limits the time that insects can enter or depart; 5) short transit time is not a critical factor for long-lived coccinellid adults; and 6) the aggregation habit of many lady beetles provides a means for significant numbers to gather on large structures, like a ship in port.

It is interesting that only two exotic aphidophagous coccinellids were found to be established during the first 67 years of this century, but that four

[6] They discussed 5 of the 6 species treated here.

more species (at five locations, one species at two different points) gained footholds in the next 20 years (Table 2). Three of these introductions probably occurred as a result of the increased ship traffic that followed the opening of the St. Lawrence Seaway in 1959 (Anon. 1991) – and the other two introductions could have benefited from the increased foreign trade that has occurred during recent years (King *et al.* 1992).

During its short life the St. Lawrence Seaway system has been the probable means of entry of 60% (3 of the 5 establishments since 1959) of the exotic coccinellids that have established in eastern North America (Table 2; the two widely-separated introduction points for *C. 7-punctata* were counted as two introductions), and this should be commented upon. Using the Seaway, ocean-going ships can travel inland 3,300 km (2,035 mi.) (Anon. 1992) through forests and farmland. This very long waterway offers a much greater opportunity for predaceous or crop-feeding insects to quickly find their hosts, compared to coastal seaports, most of which are now surrounded by urban areas which lack a variety and quantity of prey insects and agricultural food plants. While routine inspections by quarantine officials at Seaway ports may help intercept insect pests in cargo, insects that fly from a ship along the lengthy inland passage will not be excluded by this means. Although much of the St. Lawrence River has always been accessible to transoceanic ships, the opening of the Seaway immediately increased the volume of ship traffic in the river at Montreal by 62% (Matta, pers. commun.), and average ship size also increased (Anon. 1992). The amount of Seaway shipping is significant; for example, in 1991, 445 ships from foreign ports traveled inland as far as Lake Ontario (1,900 km), and 350 (79%) of them continued to westward ports, some to the maximum of 3,300 km (Anon. 1992). Moreover, ship movement is concentrated in the growing season because the Seaway system is closed during the winter (Anon. 1992).

Schaefer *et al.* (1987) suggested that, in addition to the possible introduction of *Coccinella septempunctata* L. by transoceanic ships, this species may have established in Quebec by flying from prior releases in northern Maine (400 km distant) and established in Bergen Co., NJ from earlier releases in Burlington County, NJ (80 km away). While possible, these origins appear much less likely than introduction by ships, because this beetle was never demonstrated to be established at either release site (Angalet & Jacques 1975, Shands *et al.* 1972), nor at intermediate locations, until many years after it was found close to the ports.

It has also been suggested that several of these coccinellids may have become established as a result of intentional releases by man (Gordon 1987, Wheeler 1993). However, quarantine personnel[7] verified that there were no release records for any of the six species listed in Table 2 in the areas where each was first discovered (for examples of the voluminous data maintained by each quarantine laboratory for every shipment, see Coulson 1992). While

[7] Personal communications by L.R. Ertle (U.S.A.) and M. Sarazin (Canada) to W.H.D.

undocumented releases cannot be ruled out, it is unlikely that such unauthorized releases would involve numbers of foreign coccinellids as large as in regular releases – which have had a very low rate of success in eastern North America (Angalet *et al.* 1979, Schaefer & Dysart 1988). For example, although about 150,000 laboratory-reared *C. 7-punctata* were released in 10 states and one province, permanent establishment was not verified at even one location (Schaefer *et al.* 1987).

Large numbers of laboratory-reared *P. 14-punctata* have also been released, in two different regions, with a similar lack of success. The USDA-APHIS Russian wheat aphid biocontrol project disseminated nearly 565,000 *P. 14-punctata* in 16 western states from 1987 to 1992 (Russian Wheat Aphid Biological Control Project, FY 1992 Report, D.R. Prokrym *et al.* 1993, 55 pp., unpubl.). The New Jersey Department of Agriculture released 33,500 *P. 14-punctata* adults and nearly 39,000 eggs in New Jersey, from 1989 through 1992 (R.J. Chianese, unpubl. 2 p. report, 1993). No *P. 14-punctata* has yet been recovered from the 16 western states, but this species has recently been recovered in most of northern New Jersey, as noted in Table 1. The origin of the latter establishments cannot be absolutely determined, but the evidence indicates that the southward movement of *P. 14-punctata* from New England and eastern New York was almost certainly responsible, for the following reasons: 1) the first detection in New Jersey (Warren Co., 1991) was 37 km from the nearest release point; in 1992, this beetle was found in six additional New Jersey counties, several not close to release fields and in one (Sussex) in which no releases had ever been made (but which borders New York state, where *P. 14-punctata* was discovered in six adjacent/nearby counties in 1992 (Table 1); 3) the southward movement of large numbers of *P. 14-punctata* is obvious from the recovery data in Figure 1; and 4) the comparatively small numbers released in New Jersey (33,500 beetles over the whole state vs. 239,000 acres average area per county) could not have produced detectable numbers of this univoltine beetle in 12 counties (Table 1) in such a short period of time (2-4 years and generations).

As noted in Table 2, *Harmonia axyridis* was very likely established in the U.S. via shipping, near New Orleans. It was first found there in 1988 (Chapin & Brou 1991), and was next detected at three widely-separated locations in 1990 [in both southern and northern Mississippi (Chapin & Brou 1991), and in northern Georgia (Tedders & Schaefer 1994)]. Although the latter authors suggest that this coccinellid might have established in central Georgia in 1992 as a result of releases there in 1978-1981, this is very unlikely, because: 1) detection attempts at the release locations were unsuccessful for 10 years (1982-1991); 2) *H. axyridis* was found in northern Alabama in 1991 (Tedders & Schaefer 1994) at a point directly between the northern Mississippi establishment counties and northern Georgia; and 3) the movement of *H. axyridis* had obviously gained great momentum, because this beetle reached Virginia

in early 1993 (P. W. Schaefer, pers. commun.), and by fall 1993 was collected even farther north, in Delaware (D. Paruszewski, pers. commun.), Pennsylvania (K.S. Swan, pers. commun.), and New Jersey (R.J.C., unpubl.).

Exotic coccinellids have traditionally been reared in the laboratory before release, to eliminate parasites that may be present in all four life stages. However, the above results and the summary by Gordon 1985 (Table 1: only one aphidophagous species established in the NE U.S., after attempts with 31 species) indicate that laboratory-reared exotic aphid-feeding coccinellids have not been a practical means of achieving permanent establishment. Interestingly, Gordon's Table 2 also shows that natural (not lab-reared) populations can establish themselves, and subcolonizations by man from these self-established (and preadapted) lady beetle populations have had a much better success rate, as also noted by Schaefer *et al.* 1987.

Displacement of native aphidophagous coccinellids: Day (1965) observed that *Coccinella undecimpunctata* L. was by far the most numerous coccinellid on potatoes (55% of individuals, of 14 total spp.), over a three year period, on eastern Long Island, NY. Because this is an introduced species (Table 2), it obviously had previously displaced a native ladybird which had formerly been the dominant species. Angalet *et al.* 1979 stated that the introduced *C. septempunctata* had become the dominant coccinellid on *Phragmites* plants in the Bergen County, NJ meadowlands, and Day (unpubl.) observed that this species had also become the most abundant coccinellid (of 11 spp.) on alfalfa during the 1980s. And, *H. axyridis* is now the dominant lady beetle in a pecan orchard in Georgia (Tedders & Schaefer 1994). These examples indicate that substantial displacement of native lady beetles by exotic species has occurred in the eastern U.S. Although some people are concerned about the intentional or accidental introduction of exotic predators, historical evidence indicates that competitive displacement is likely only when the replacing species is superior in one or more attributes, that a higher degree of prey suppression will result (Huffaker & Messenger 1976), and native predator species do survive.

In any event, accidental introductions cannot be prevented, and we agree with Schaefer & Dysart (1988) that more will occur in the future, if intercontinental commerce continues at the present high levels. And, because all of the six adventive coccinellids were discovered by chance, it is possible that other exotic species may be present – but undetected. As Wheeler 1992 has pointed out, "Prompt detection of immigrants and surveys to document their dispersal" are often neglected, leading to later confusion and uncertainty as to origin and points of introduction – both of which may later be of considerable importance. The CAPS program, a cooperative effort between USDA-APHIS and all the States, provides a means for promptly discovering newly established pest and beneficial insect species, and hopefully this important work can be continued.

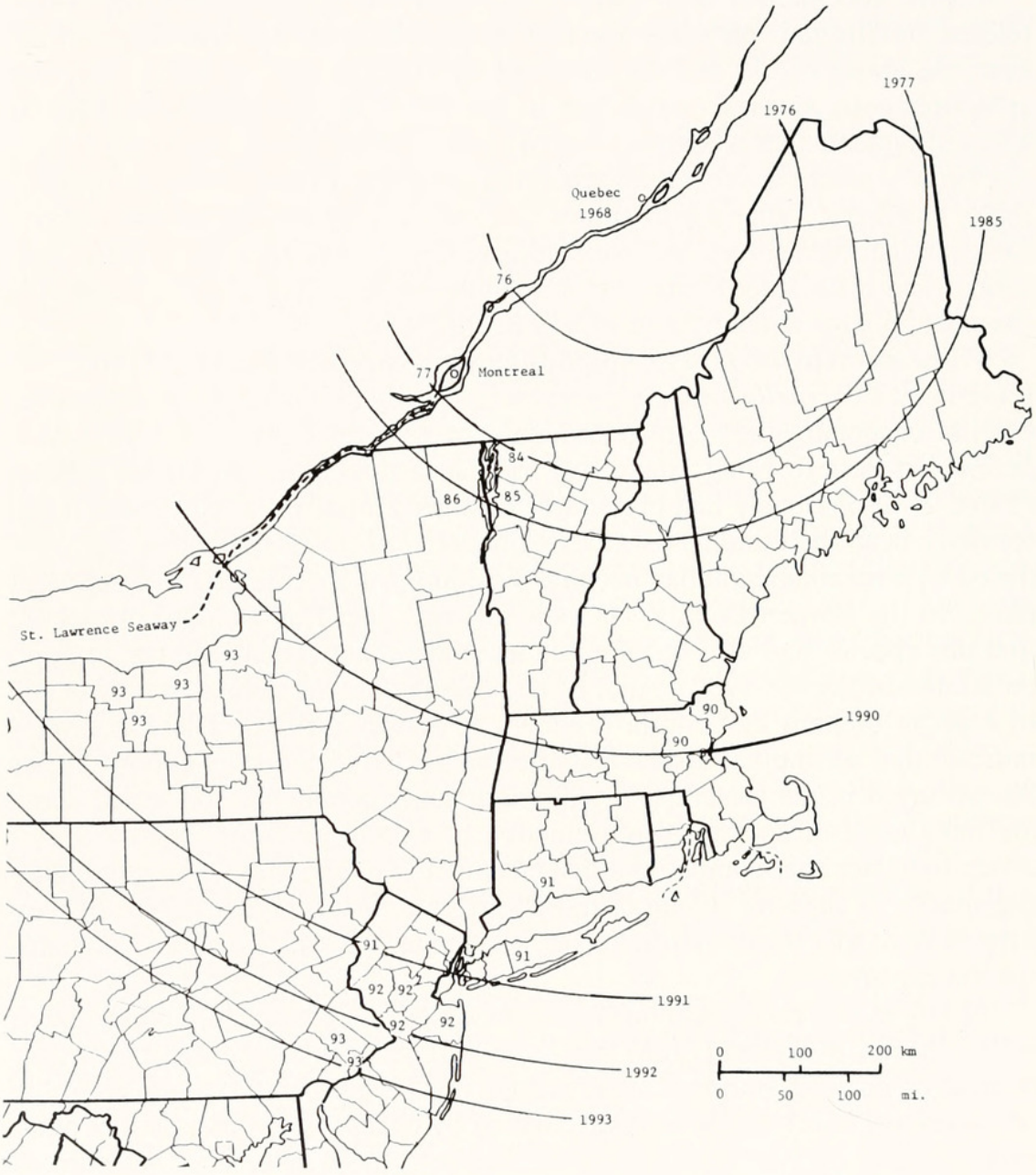

Figure 1. The southward advance of *Propylea 14-punctata* (L.). The number within a county is the year that this species was first detected there. Only "leading edge" county records or new area discoveries are included. The arcs represent maximum dispersion.

Table 1. First recoveries of *Propylea quatuordecimpunctata* (L.) from states and counties in the northeastern United States.

State	County	Date	Collector	Collected on	Sampling method
CT	Fairfield	5/20/92	D. Comboni	roadside	visual
	Hartford	6/17/92	D. Ellis	grasses, weeds	sweep net
	Litchfield	6/14/93	G. Moseley	tomato	pheromone trap
	Middlesex	6/10/93	D. Ellis	alfalfa	sweep net
	New Haven*	8/26/91	D. Ellis	crabapple	Ladd trap
	New London	7/16/92	D. Ellis	alfalfa	sweep net
	Tolland	5/21/92	D. Ellis	alfalfa	sweep net
	Windham	7/16/92	D. Ellis	broccoli	pheromone trap
MA	Berkshire	8/26/93	S. Maisey	alfalfa, weeds	sweep net
	Bristol	6/08/93	D. Fernandez	alfalfa, weeds	sweep net
	Essex	7/30/90	Karen Idoine	sweet corn	visual
	Franklin	9/12/92	A.G. Wheeler[a]	weeds	sweep net
	Hampden	6/25/93	S.A. Maisey	alfalfa	sweep net
	Hampshire	9/18/92	C. Hollingsworth	sweet corn	yellow sticky trap
	Middlesex*	6/19/90	Gary Couch	burdock	visual
	Norfolk	5/22/91	Karen Idoine	*Euonymus*	visual
	Plymouth	6/08/93	D. Fernandez	alfalfa	sweep net
	Worcester	9/18/92	C. Hollingsworth	sweet corn	yellow sticky trap
ME	Androscoggin	9/13/93	R. Mack	weeds	sweep net
	Aroostook	7/05/89	A.G. Wheeler[a]	speckled alder	branch beating
	Cumberland	7/15/91	D. Barry	sweet corn	sweep net
	Franklin	9/16/93	R. Mack	weeds	sweep net
	Hancock	9/02/93	R. Mack	weeds	sweep net
	Kennebec*	6/07/88	M.P. Tully[b]	raspberry	
	Knox	7/07/92	D. Comboni	weeds	visual
	Lincoln	9/13/93	R. Mack	weeds	sweep net
	Oxford	7/02/93	D. Barry	alfalfa	sweep net
	Penobscot	7/03/89	A.G. Wheeler[b]	hairy vetch	sweep net
	Piscataquis	9/08/93	R. Mack	weeds	sweep net
	Sagadahoc	9/13/93	R. Mack	weeds	sweep net
	Somerset	9/08/93	R. Mack	weeds	sweep net
	Waldo	9/02/93	R. Mack	weeds	sweep net
	Washington	9/07/93	R. Mack	weeds	sweep net
	York	7/24/91	D. Barry	sweet corn	sweep net
NH	Belknap	7/14/93	D. Barry N. Smith	sweet corn	earworm trap
	Carroll	8/11/93	S. Reynolds J.S. Weaver	alfalfa	sweep net
	Cheshire	6/23/93	S. Longsjoe	alfalfa	sweep net
	Coos	8/05/93	L. Wallace	sweet corn	corn earworm trap
	Grafton	9/12/92	A.G. Wheeler[a]	weeds	sweep net
	Hillsborough	6/29/93	S. Reynolds J.S. Weaver	alfalfa	sweep net
	Merrimac	6/12/93	A.T. Eaton	weeds	sweep net
	Rockingham	7/10/91	D.S. Chandler	unknown	unknown

State	County	Date	Collector	Collected on	Sampling method
	Strafford*	6/27/90	J.S. Weaver	alfalfa	sweep net
	Sullivan	7/30/93	D. Barry B. Nelson	sweet corn	corn earworm trap
NJ	Bergen	6/7/93	J. VonderHorst	weeds	sweep net
	Burlington	7/27/93	W. Peaslee	alfalfa	sweep net
	Essex	6/7/93	J. VonderHorst	grass	sweep net
	Hunterdon	6/09/92	H. Crowley	alfalfa	sweep net
	Mercer	5/12/92	R. Chianese	alfalfa	sweep net
	Middlesex	6/09/93	J. VonderHorst	weeds	sweep net
	Monmouth	7/03/92	M. Mayer	weeds	sweep net
	Morris	7/10/92	E. Stern	alfalfa, clover	sweep net
	Passaic	6/03/93	J. VonderHorst	grasses	sweep net
	Somerset	5/29/92	H. Crowley	clover	sweep net
	Sussex	7/16/92	W.H. Day	red & white clov.	sweep net
	Warren*	7/31/91	W.H. Day	alfalfa	sweep net
NY	Albany	9/11/92	A.G. Wheeler[a]	weeds	sweep net
	Clinton*	6/01/86	R.J. Dysart[c]	alfalfa, vetch	sweep net
	Dutchess	7/12/92[d]	W.H. Day	alfalfa	sweep net
	Essex	6/11/91	Alan Letterman	grass, clover	sweep net
	Franklin	6/07/90	Alan Letterman	vetch	sweep net
	Lewis	8/18/93	J. Knodel	red clover	sweep net
	Monroe	8/05/93	J. Knodel	red clover	sweep net
	Ontario	8/05/93	J. Knodel	red clover	sweep net
	Orange	7/11/92[d]	W.H. Day	alfalfa	sweep net
	Oswego	8/18/93	J. Knodel	red clover	sweep net
	Putnam	9/19/92	A.G. Wheeler[a]	weeds	sweep net
	Rensselaer	9/11/92	A.G. Wheeler[a]	weeds	sweep net
	Saratoga	9/13/92	A.G. Wheeler[a]	weeds	sweep net
	St. Lawrence	6/13/90	Alan Letterman	clover, vetch	sweep net
	Suffolk	6/26/91	Janet Knodel	sweet corn	visual
	Warren	9/13/92	A.G. Wheeler[a]	weeds	sweep net
	Washington	9/13/92	A.G. Wheeler[a]	weeds	sweep net
	Wayne	7/23/93	J. Knodel	cabbage	pheromone trap
PA	Bucks	7/16/93	R.L. Stewart[e]	alfalfa	sweep net
	Lehigh	8/13/93	R.L. Stewart	alfalfa	sweep net
	Monroe	6/18/93	R.L. Stewart[e]	alfalfa	sweep net
	Montgomery	8/26/93	R.L. Stewart	clover	sweep net
	Northhampton	6/21/93	R.L. Stewart[e]	alfalfa	sweep net
	Philadelphia	6/17/93	Wheeler & Stewart[e]	weeds	sweep net
	Pike*	6/15/93	Wheeler & Stewart[e]	weeds	sweep net
	Wayne	8/31/93	R.L. Stewart	alfalfa	sweep net
RI	Bristol	9/17/92	Lisa Tewksbury	sweet corn	yellow sticky trap
	Newport*	8/14/92	Lisa Tewksbury		pheromone trap
	Providence	9/17/92	Lisa Tewksbury	sweet corn	yellow sticky trap

State	County	Date	Collector	Collected on	Sampling method
VT	Addison	5/20/91[d]	J. Turmel	alfalfa	sweep net
	Bennington	6/28/93	J. Turmel	alfalfa, clover	sweep net
	Caledonia	7/08/93	J. Turmel	alfalfa, clover	sweep net
	Chittenden	?/?/85[d]	B.L. Parker[c]	alfalfa	sweep net
	Essex	6/19/93	J. Turmel	alfalfa, clover	sweep net
	Franklin	7/15/93	J. Turmel	alfalfa, clover	sweep net
	Grand Isle*	8/17/84	B.L. Parker[c]	alfalfa	sweep net
	Lamoille	9/20/93	J. Turmel	alfalfa, clover	sweep net
	Orange	5/25/93	J. Turmel	alfalfa, clover	sweep net
	Orleans	7/08/93	J. Turmel	alfalfa, clover	sweep net
	Rutland	9/13/92	A.G. Wheeler[a]	weeds	sweep net
	Washington	9/12/92	A.G. Wheeler[a]	weeds	sweep net
	Windham	9/12/92	A.G. Wheeler[a]	weeds	sweep net
	Windsor	6/28/93	J. Turmel	alfalfa	sweep net

*First collection in state. This species was first found in the United States in 1984.

[a] Reported in Wheeler, 1993.

[b] Reported in Wheeler, 1990.

[c] Reported in Dysart, 1988.

[d] This is an earlier collection than that cited in Wheeler, 1993.

[e] Personal Communication to W.H.D., from A.G. Wheeler, Jr., 8/93.

Table 2. Foreign aphidophagous Coccinellidae that are now established in eastern North America.

Species	First Collection			Previous release	Probable entry[m]
	Year	State/Prov.	County/Parish		
Coccinella undecimpunctata L.	1912[a]	Massachus.	Suffolk	None[h]	Port of Boston
Harmonia quadripunctata (Pontopiddian)	1924[b]	New Jersey	Passaic	None[h]	New York/New Jersey ports
Propylea quatuordecimpunctata (L.)	1968[c]	Quebec	Quebec	None[i]	Quebec City port, SLR (St. Lawrence River)
Coccinella septempunctata L.	1973[d]	New Jersey	Bergen	80km (48mi.)[j]	Ports of Jersey City /Elizabeth , NJ
	1973[e]	Quebec	L'Assomption	None[k]	SLR, near Montreal
Hippodamia variegata (Goeze)	1984[f]	Quebec	Shefford	None[i]	Port of Montreal, SLR
Harmonia axyridis (Pallas)	1988[g]	Louisiana	St. Tammany	360km[l] (215 mi.)	Port of New Orleans

[a] Schaeffer, 1912.

[b] Vandenberg, 1990.

[c] Chantal, 1972.

[d] Angalet and Jacques, 1975.

[e] Larochelle, 1979.

[f] Gordon, 1987.

[g] Chapin and Brou, 1991.

[h] No release on record for the U.S.: Clausen *et al.* 1978, Ertle (pers. commun.).

[i] No release on record for Canada: Clausen *et al.* 1978, Corbet & Prentice 1971, Sarazin (pers. commun.).

[j] 112 females released in Hunterdon Co. in 1959 (Ertle, pers. commun.); species not detected here until 1977 (Angalet *et al.* 1979). Also released in Burlington Co. (4,500 females in 1958-59, and 428 females in 1964; this is 117 km/70 mi. from Bergen Co.) but species not detected here until ca. 1978 (estimated from data in Angalet *et al.* 1979).

[k] ca. 25 females were released in New Brunswick in 1959-1960, and ca. 65 females in Nova Scotia in 1960 & 1967 (Corbet & Prentice 1971). These locations are far from the 1973 recovery site NE of Montreal (525 km/350 mi. and 750 km/450 mi., respectively), there was no post-release recovery at these locations (Corbet & Prentice 1971), and the very small numbers all make a connection to the 1973 Quebec recoveries (Larochelle 1979) very unlikely.

[l] 16 females released near Shreveport, LA in 1979 (380 km/230 mi. NW of recovery site) (Ertle, pers. commun.), and ca. 1,900 females near Leland, MS in 1980 (360 km/215 mi. N of recovery site) (Ertle, pers. commun.) *H. axyridis* was not found at either release site through 1990 (Chapin & Brou 1991).

[m] Based on absence of nearby (within 167 km/100 mi.) releases for 6 of 7 examples, and data given (j above) for the 7th example.

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