# CHANGES IN ABUNDANCE OF NATIVE AND ADVENTIVE COCCINELLIDAE (COLEOPTERA) IN ALFALFA FIELDS, IN NORTHERN NEW JERSEY (1993-2004) AND DELAWARE (1999-2004), U.S.A.<sup>1</sup>

### W. H. Day<sup>2</sup> and K. M. Tatman<sup>2</sup>

ABSTRACT: Weekly and biweekly sweep net collections were made near Blairstown, New Jersey, and Newark, Delaware (both in the U.S.A.), for 12 and 6 consecutive years, respectively. At Blairstown, only one non-native coccinellid [Coccinella septempunctata (L.)] was common when this research was started in 1993, one [Propylea quatuordecimpunctata (L.)] had recently appeared, and two others [Harmonia axyridis (Pallas), Hippodamia variegata (Goeze)] were detected later during the 12-year study. All of these four species were adventive, having established themselves through commerce, three species at inland ports, and one near a coastal seaport. The most numerous adult lady beetles at both locations were two native species, Coleomegilla maculata (F.) and Hippodamia parenthesis (Say), and three adventive species, P. quatuordecimpunctata, C. septempunctata, and H. axyridis. Six species were occasionally swept at Blairstown - one adventive species (H. variegata) and five native species [Cycloneda munda (Say), Coccinella transversoguttata Mulsant, C. trifasciata Mulsant, Hippodamia convergens Guerin, and Brachiacantha ursina (F.)]. All but the last species were also found at Newark. Lady beetle numbers varied considerably from year to year at both locations, demonstrating that long-term (10 years or more) research is required to correctly identify population trends. No coccinellid species decreased during the 12-year study at Blairstown-indicating that the once-common H. convergens and several species of Coccinella had become rare before the study started in 1993, and before three of the four adventive lady beetles had become numerous. The previous establishment of exotic parasites, previously reported to have reduced pea aphid numbers, was likely indirectly responsible for decreasing coccinellid diversity in alfalfa. Competition by the adventive C. septempunctata may also have reduced some coccinellid species prior to 1993, but such data for the northeastern U.S.A. have not been published, to our knowledge.

KEY WORDS: Coccinellidae, changes in abundance, native, adventive, New Jersey, Delaware, U.S.A.

Most aphid-feeding coccinellids are large and brightly colored, unlike most other predators and parasites of aphids, so they have been recognized as important natural enemies of pest aphids for more than 150 years (Kirby and Spence 1860). Recently, interest in these beetles has increased, as several once-common native lady beetles have become rare (e.g. Wheeler and Hoebeke 1995, Ellis et al. 1999). Because several foreign coccinellids have become established in North America through commerce since the early 1970s, some of these new arrivals have been considered responsible for displacing native lady beetles in some areas (Turnock et al. 2003, Wheeler and Hoebeke 1995), but not in others (Wright and DeVries 2000). Many major pest insects have become established in North America via shipping, and although it is less well known, this also has happened with predators and parasites of insects (Sailer 1978).

Changes in natural enemy dominance usually evolve over many years, requiring long-term studies to determine the eventual outcome (Day 2005). The research reported here was conducted in alfalfa, a relatively stable perennial crop, at two locations, over 6- and 12-year periods. The principal prey of lady

<sup>&</sup>lt;sup>1</sup>Received on January 16, 2006. Accepted on March 30, 2006.

<sup>&</sup>lt;sup>2</sup> USDA-BIRL, 501 Chapel Street, Newark, Delaware 19713 U.S.A. Email: william.day@ars.usda. gov.

beetles in alfalfa is the pea aphid [*Acyrthosiphon pisum* (Harris)], an adventive insect that had become so abundant by the late 1800s that it was a serious pest of peas (Sanderson 1900), and often was a significant pest of alfalfa for many years in North America (Kindler et al., 1971). In contrast, soon after the establishment of two parasites introduced by the USDA, damaging pea aphid populations in northeastern alfalfa became rare (Angalet and Fuester 1977, Day unpublished).

When this study was begun in 1993, two non-native coccinellid species were already present in the Blairstown, NJ, study area (NW New Jersey). Only one species was numerous, however, because the second species had only recently arrived (1991). Two more foreign lady beetles reached this area in 1994 and 1997, so a total of four non-native species were present there during the final seven years of the study.

This paper describes both the changes and the lack of changes in the coccinellid fauna of the piedmont area of northwestern New Jersey during this 12year period. For comparison, data for the final six years of observations (1999-2004) are included from alfalfa at a second location - Newark, DE, located on the coastal plain in northern Delaware, 100 miles to the south.

#### METHODS

Coccinellid adults were collected in alfalfa fields using a sweep net, near Blairstown, New Jersey (41° 00' N, 74° 54' W, elevation 160-290m), and at Newark, Delaware (39° 40' N, 75° 44' W, elev. 33m). Three alfalfa fields were sampled each week (May-July), or biweekly (August-October) for 12 years at Blairstown, and one alfalfa field was sampled each week (May-October) for six years at Newark. Each sweep sample consisted of 100 half-cycles. If a field had recently been mowed, another adjacent or nearby alfalfa field was sampled until the original field had regrown. When a field was rotated to another crop, which occurred at 5-8 year intervals, an adjacent or nearby alfalfa field was substituted. The Blairstown data are averages of three fields.

Contents of the sweep nets were emptied into a glass-topped sleeve cage, to prevent escape of the coccinellids as they were being aspirated into clear plastic vials for counting and identification to species. All lady beetle species were identified by the authors. Voucher specimens are in the reference collection at the USDA Newark laboratory.

To reduce bias at each location, all samples at Blairstown were collected by the first author, and all Newark sampling was done by the second author.

### **RESULTS AND DISCUSSION**

**Non-native species.** Four non-native coccinellid species were collected in the sampled fields at both locations. The years and locations of first detection and the methods of entry of these species are summarized in Table 1. Although two of these species, *C. septempunctata* (L.) and *H. axyridis* (Pallas), had been previ-

ously released in North America, a careful comparison of published and quarantine records indicate (Gordon 1985, Table 2; Day et al., 1994, Table 2) that neither species became established where it had been released, and that all four species became established accidentally elsewhere, at or near seaports. These species are referred to in this paper as "adventive," to differentiate them from "introduced" species, because the latter term implies establishment by intentional importation and release.

Although *C. septempunctata* (7-punctata, hereafter) had reached both study areas in the 1970s, the other three species (Table 1) did not arrive until the 1990s. Two additional adventive coccinellids, *Coccinella undecimpunctata* L. (Wheeler and Hoebeke 1981) and *Harmonia quadripunctata* (Pontoppidan) (Hoebeke and Wheeler 1996), have been found elsewhere in the northeastern U.S., but were not detected at either of our study locations.

**Major species in alfalfa.** The most commonly collected coccinellid species over all years are listed in Table 2. It is interesting that the five most numerous species were the same at both locations, despite the latitude and elevation differences mentioned earlier. Because three of the five most numerous species at both locations are adventive, it is probable that additional lady beetle species (as reported for alfalfa by Angalet and Fuester 1977, Ellis et al., 1999, Wheeler and Hoebeke 1995, and others) were abundant before these new arrivals appeared, but unfortunately prior data from our two study locations have not been published, to our knowledge.

A bar graph (Fig. 1) of these data shows the numerical relationships more clearly. A native coccinellid, *Coleomegilla maculata* (F.), was the most abundant species at both locations—strikingly so at Newark, perhaps because of nearby field corn, which was absent from two of the three Blairstown farms. This beetle has long been a dominant species in corn (Forbes, 1883; Wright and DeVries 2000), probably because it can survive there on pollen and fungus spores, so is less dependent on availability of aphids (Forbes 1883). Moreover, Day (unpubl.) once observed an adult inside a corn kernel, eating the contents.

All of the three most numerous lady beetle species [*C. maculata, P. quatuordecimpunctata* (L.), *H. parenthesis* (Say)] (Fig.1) are small (mean length 4.8mm), about 1/3 smaller than the two less numerous species (*C. 7-punctata, H. axyridis*; mean length 7.0mm). Perhaps more small coccinellids can be produced from a given number of aphids than large coccinellids, contributing to the observed greater abundance of the smaller species.

| 1st OBSEI                       | RVED IN      | 1st OBSERVED IN EASTERN NORTH AMERICA <sup>a</sup>               | MERICA <sup>a</sup>  | 1st        | 1st OBSERVED IN UNITED STATES | TED STATES           | 1st detected      | cted              |
|---------------------------------|--------------|--|--|------------|-------------------------------|----------------------|-------------------|-------------------|
| Species                         | Year         | Location   | Reference  | Year       | Location                      | Reference            | Ŋ                 | DE                |
| Coccinella 7-punctata<br>(L.)   | 1973<br>1973 | E. Rutherfordb, NJ<br>Repentigny, Quebec                         | Angalet and Jacques 1975<br>Larochelle 1979  | 1973       | E. Rutherford, NJ             | A. and J. 1975       | 1975 <sup>c</sup> | 1977              |
| Propylea 14-punctata<br>(L.)    | 1968         | Quebec City, Quebec  | Chantel 1972   | 1984       | Grande Isle, VT               | Dysart 1988          | 1991              | 1997 <sup>e</sup> |
| Harmonia axyridis<br>(Pallas)   | 1988         | near New Orleans, LA   | near New Orleans, LA Chapin and Brou 1991  | 1988       | Abita Springs, LA             | C. and B. 1991       | 1994              | 1993              |
| Hippodamia variegata<br>(Goeze) | 1984         | Montreal, Quebec   | Gordon 1987  | 1992       | NY and VT                     | Wheeler 1993         | b7991             | 1994 <sup>e</sup> |
| ~                               |              |  |  |            |                               |                      |                   | 1                 |
| a All four species wer          | e first det  | ected near major seaports  | <sup>a</sup> All four species were first detected near major seaports. Four of the five locations (except East Rutherford, near Elizabeth, NJ) are inland ports. Two species | ept East I | Rutherford, near Eliza        | beth, NJ) are inlan  | 9                 | d ports. Tw       |
| had never been relea            | ised in No   | orth America; the other tw                                       | had never been released in North America; the other two species had never been detected at any of their release locations, which were 80-360 km from their                   | ted at any | / of their release locat      | ions, which were 80  | -360 km           | Ð                 |
| first recovery sites (c         | details are  | first recovery sites (details are in Day et al., 1994, Table 2). | e 2).  |            |                               |                      |                   |                   |
| b This is the closest town      | wn to the    | first detection site som   | to the first detection site — some references refer to the "Hackensack meadowlands," a large marsh which extends through several New   | isack mea  | ıdowlands," a large ma        | ırsh which extends t | hrough sev        | eral New          |
| Jersey towns.                   |              |  |  |            |                               |                      |                   |                   |
| c This is the only adve         | entive spe   | cies that was numerous w   | c This is the only adventive species that was numerous when observations were started in NJ in 1993.   | NJ in 19   | 193.                          |                      |                   |                   |
| d First recorded collec         | tion at Bl   | airstown; this species was                                       | d First recorded collection at Blairstown; this species was found in an adjacent county (Sussex) much earlier (1993).  | ussex) m   | uch earlier (1993).           |                      |                   |                   |
| Apparentity unocuri             | ILI NATIA    | ine illerature: uiese two u                                      | · Apparently undocumented in the interature: these two dates are from unpublished USDA-newark records.   | -INCWALL   | V LECOLUS.                    |                      |                   |                   |

| Locations      | Species                                       | $\overline{x}$ no.<br>/100<br>sweeps | years<br>present |
|----------------|---|--------------------------------------|------------------|
| Blairstown, NJ | Coleomegilla maculata (F.)                    | 1.27                                 | 12               |
| (1993-2004)    | Propylea 14-punctata <sup>b</sup> (L.)        | 1.13                                 | 12               |
|                | Hippodamia parenthesis (Say)                  | 0.51                                 | 12               |
|                | Coccinella 7-punctata <sup>c</sup> (L.)       | 0.30                                 | 12               |
|                | Harmonia axyridis (Pallas)                    | 0.22                                 | 11               |
| Newark, DE     | Coleomegilla maculata (F.)                    | 3.47                                 | 6                |
| (1999-2004)    | Hippodamia parenthesis (Say)                  | 0.83                                 | 6                |
|                | <i>Propylea 14-punctata</i> <sup>b</sup> (L.) | 0.76                                 | 6                |
|                | Harmonia axyridis (Pallas)                    | 0.65                                 | 6                |
|                | Coccinella 7-punctata <sup>c</sup> (L.)       | 0.43                                 | 6                |

 Table 2. Major<sup>a</sup> coccinellid species collected in alfalfa at two locations

<sup>a</sup> Average number was more than 0.2 adults per 100-sweep sample, calculated over all collection dates and fields (Fig. 2), during the 1993-2004 (Blairstown), and 1999-2004 (Newark) growing seasons (May-October).

<sup>b</sup> The full species name is *quatuordecimpunctata*.

<sup>c</sup> The full species name is *septempunctata*. The two abbreviated species names are used in this paper for brevity. Adventive species are in **bold** type.

**Minor species in alfalfa.** Six to seven additional coccinellid species (Table 3) were usually present in small numbers, during the 6- and 12-year observation periods. *H. convergens* Guerin, an abundant native species in alfalfa in some locations (Elliott et al., 1996, Turnock et al., 2003), was never numerous at Blairstown or Newark, nor was *H. variegata* (Goeze), an adventive species. Details on other seldom-collected species are also in Table 3. If any of the native coccinellids had been reduced by the arrival of adventive lady beetles at Blairstown prior to the initiation of this study in 1993, only *C. 7-punctata* could have been responsible, because other adventive species were not yet numerous, or had not yet become established (Table 1).

**Changes in coccinellid species following arrival of adventive lady beetles.** Because *C. 7-punctata* was first detected at Blairstown 16 years before this study was started, and three other coccinellids arrived two years prior to four years after this study began, we recognized that it would be difficult to determine the causes of all changes that might be observed, and their significance. We also recognized that the six years of data from Newark, while useful for comparisons to Blairstown, are insufficient to detect changes in abundance of coccinellids, which vary considerably from year to year (Wheeler 2003). "Before-after" comparisons were therefore only made for Blairstown, comparing two, five-year time periods—before most adventive coccinellids were abundant (1993-1997), and after (2000-2004). Figure 2 compares "before" to "after" abundances for both native and adventive lady beetles. There was an unexpected increase in the total number of native coccinellids (2A), nearly all of which was an increase in *C. maculata*, but this change was not statistically significant. Similarly, there was an increase in the total number of all adventive lady beetles (also not statistically significant), that was nearly entirely composed of a large increase in *P. quatuordecimpunctata* (*P. 14-punctata*, hereafter) (2B, which was significant at the 1% level).

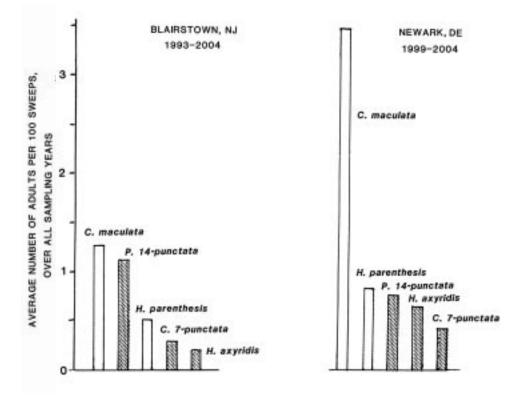


Figure 1. Average abundance of the 5 major coccinellid species in alfalfa at 2 locations, over all years. Shaded bars = adventive species.

| Locations                     | Species  | spp.                    | x no.<br>/100<br>sweeps              | Years                   |
|-------------------------------|--|-------------------------|--------------------------------------|-------------------------|
| Blairstown, NJ<br>(1993-2004) | Hippodamia spp. <sup>b</sup><br>Cycloneda munda (Say)<br>Brachiacantha ursina (F.)<br>Coccinella spp. <sup>c</sup> | 2<br>1<br>1<br>3/7      | 0.091<br>0.037<br>0.023<br>0.007     | 8, 12<br>12<br>12<br>12 |
| Newark, DE<br>(1999-2004)     | Hippodamia spp. <sup>b</sup><br>Cycloneda munda (Say)<br>Coccinella spp. <sup>c</sup>                              | 2<br>1<br><u>3</u><br>6 | 0.343 <sup>d</sup><br>0.023<br>0.000 | 6<br>6<br>6             |

Table 3. Minor<sup>a</sup> coccinellid species collected in alfalfa at two locations

<sup>a</sup> "Minor" lady beetle species were, on average, much less numerous than the "major" five species in Table 2.

<sup>b</sup> Includes *H. variegata* (Goeze) (an adventive species present for 8 years at Blairstown and all 6 years at Newark) and *H. convergens* Guerin, a native species that was uncommon at both locations.

<sup>c</sup> Includes *C. transversoguttata* Mulsant, *C. 9-notata* Herbst, and *C. trifasciata* Mulsant. The once-common *C. 11-punctata* (L.) was not detected at either location.

<sup>d</sup> Listed as "minor" because this genus was abundant in only one year (2002), and at only one of the two locations. Adventive species are in **bold** type.

It is important to note that only one (*P. 14-punctata*) of the four adventive coccinellid species became more numerous between these two time periods (Fig. 2), while the other three immigrant species remained at low levels. This included *C. 7-punctata*, which had become the dominant lady beetle in Manitoba alfalfa by 1992 (Turnock et al., 2003), in S. Dakota alfalfa by 1988-1992 (Elliott et al., 1996), and at its initial New Jersey establishment locale in the 1970s (Angalet et al., 1979). However, it was a minor coccinellid species in Nebraska alfalfa in 1992-1995 (Wright and DeVries 2000). These major differences in coccinellid species rankings within the same crop grown in widely separated areas indicate that the eventual importance of "new" coccinellid species, whether introduced intentionally or accidentally, is not predictable. Moreover, the outcomes in alfalfa are not necessarily the same as in other crops, such as apple trees (Brown and Miller 1998) and corn (Elliott et al., 1996).

**Possible causes of changes in abundance of some coccinellid species.** Because three of the five most numerous lady beetle species were adventive species (Fig. 1), other native coccinellids may have been more numerous prior to the arrival of the invading species. The "competitive displacement" that apparently caused the scarcity of many native lady beetles [including *Coccinella*  novemnotata Herbst (C. 9-notata, hereafter), C. transversoguttata Mulsant, C. trifasciata Mulsant, Hippodamia convergens, and H. tredecimpunctata] has been widely discussed as a possible result of the establishment of C. 7-punctata (e.g. Angalet and Fuester 1977, Brown and Miller 1988, Ellis et al., 1999, Elliott et al., 1996, Stephens 2002a, Wheeler and Hoebecke 1995, Wheeler and Stoops 1996). However, it is well to keep in mind the following points: "correlation does not prove causation" (a similar caution was made by Wheeler and Hoebeke 1995), C. 7-punctata was not a dominant species (it was 4th or 5th in numbers) in the present study, and native coccinellids were first and second (Newark) to first and third (Blairstown) in abundance (Fig. 1) in this study.

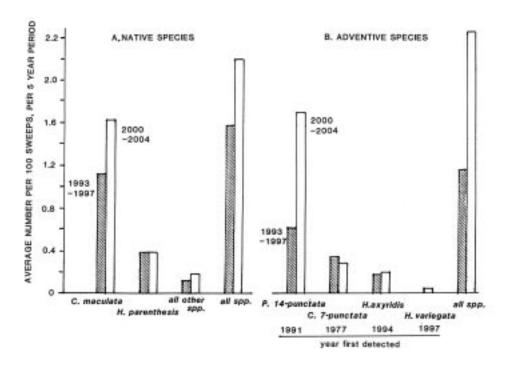


Figure 2. Comparative abundance of native and adventive coccinellid species during two 5-year periods (1993-1997 vs. 2000-2004), in northern New Jersey. The only statistically – significant change was the increase in *P. 14-punctata* (ANOVA: F=16.9; d.f. 8, 1; P=0.01).

An additional complicating factor may be the large reductions in pea aphid numbers that occurred in the 1960s and 1970s following the USDA biocontrol program which resulted in the widespread establishment in the U.S. of the parasites Aphidius smithi Sharma and Subba Rao and A. ervi Haliday (Angalet and Fuester 1977). The resulting lower food supply (much reduced pea aphid populations in alfalfa and pea crops over 21 years: Angalet and Fuester 1977) would be expected to reduce coccinellid numbers (fewer aphids was one of the hypotheses also advanced by Wheeler and Hoebeke 1995), and could affect some species more than others, but to our knowledge these effects have not been documented by published field studies. We were able to find one example of unpublished data: during the period when the introduced Aphidius parasites of the pea aphid were spreading rapidly over the United States and Canada (Angalet and Fuester 1977), G. W. Angalet (USDA-Moorestown, New Jersey) collected 137 samples of coccinellids in alfalfa fields in several states, during 1966-1969. A recent compilation of his data by Stephens (2002b) showed that Coccinella 9notata had become scarce (0-1% of all lady beetles) by 1968-1969. Because this occurred 4-5 years before C. 7-punctata was first detected (1973) in a small area in coastal New Jersey, competition by the latter adventive coccinellid could not have been involved.

**Changes in the total number of coccinellids over time.** When the total of all species per sample, each year, was tabulated (Fig. 3), several interesting patterns emerged. First, the year to year variations in beetle numbers during the 12-year period at Blairstown confirms Wheeler's (2003) statement about the considerable amount of variability from one year to another. And, the usually alternating "high-low" fluctuations suggest that, when very numerous, these beetles depressed the numbers of their aphid prey, so the aphids were usually much less abundant in the next year, which in turn reduced the coccinellids.

The third pattern was the unexpected gradual increase in total lady beetle numbers from 1993 to 2002, which was shown above to have been due to increases in two small coccinellid species (Fig. 2) – one native (*C. maculata*) and one adventive (*P. 14-punctata*).

Finally, because the high numbers of beetles in 2002 in northern New Jersey (Blairstown) also occurred in Delaware (Newark) (Fig. 3), and the population fluctuations from 1997-2004 were surprisingly similar at both locations, there appears to be an as yet unknown regional influence on aphid and/or lady beetle numbers – perhaps due to weather effects, directly on these insects or indirectly through the host plant.

**Life cycle observations.** When the total number of each of the five major coccinellid species over all years at Blairstown was plotted for each month (Fig. 4), it was evident that only *H. axyridis* appeared to produce two generations during the year, as evidenced by two population peaks. This graph also suggests temporal differences – *C. 7-punctata* and *P. 14-punctata* were most numerous in early summer, while *C. maculata* appeared in late summer, possibly after its aphid prey had declined on corn.

**Significant Findings.** During this 12-year field study, only five coccinellid species (two native and three adventive) were abundant in alfalfa. One native and one adventive species became more numerous during the study; both are smaller than the other three species. Although *Coccinella 7-punctata* was the only adventive lady beetle that had been present for many years before these observations were started, it was not one of the dominant species before or after the other three adventive coccinellids became well established. Five species of lady beetles previously recorded from alfalfa in other areas were absent or rarely sampled in northwestern New Jersey alfalfa, even in the early 1990s when three of the four adventive species were uncommon or absent. These findings indicate that long-term (over a decade) field studies, in the same crop and area, are necessary to document and understand the changes that occur.

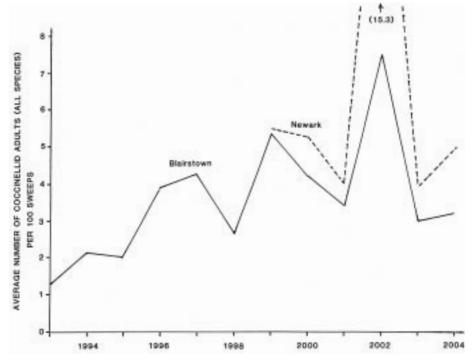


Figure 3. Total number of coccinellid adults (all species) swept in alfalfa, at Blairstown, NJ (1993-2004) and Newark, DE (1999-2004).

**Unanswered questions.** It is unclear whether the five native coccinellid species that were seldom collected during this study had been previously reduced by competition with *Coccinella 7-punctata*, or by the reduction in pea aphids which followed the establishment of two introduced *Aphidius* parasites. The causes of the similar and nearly cyclic fluctuations of all coccinellid species at both study locations are also unknown.

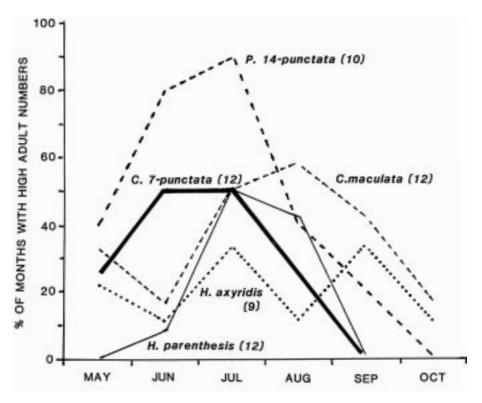


Figure 4. Estimated number of generations: percentages of months with high numbers of coccinellid adults at Blairstown, NJ 1993-2004. The number of years with data sufficient to include are in parentheses.

## ACKNOWLEDGMENTS

We thank R. W. Fuester, P. W. Schaefer, R. L. Tatman, and the anonymous reviewers for suggesting improvements to the manuscript; B. R. Holmes for typing; the following growers who allowed us to sample insects on their farms: H., J., and D. Crisman; G. W. and G. H. Fee; G. Teel, W. Vosper, and J. Vough (Blairstown, New Jersey); T. Timko, J. Hummel, and S. Hopkins for cultural assistance (Newark, Delaware); and M. Sarazin (Canada) and L. R. Ertle (U.S.A.) for carefully examining official records for evidence of releases of non-native coccinellids prior to their detection in eastern North America.

### LITERATURE CITED

- Angalet, G. W. and R. L. Jacques. 1975. The establishment of *Coccinella septempunctata* L. in the continental United States. Cooperative Economic Insect Report 25: 883-884.
- Angalet, G.W. and R. W. Fuester. 1977. The *Aphidius* parasites of the pea aphid *Acyrthosiphon pisum*, in the eastern half of the United States. Annals of the Entomological Society of America 70: 87-96.
- Angalet, G. W., J. M. Tropp, and A. N. Eggert. 1979. Coccinella septempunctata in the United States: recolonization and notes on its ecology. Environmental Entomology 8: 896-901.
- Brown, M. W. and S. S. Miller. 1998. Coccinellidae (Coleoptera) in apple orchards of eastern West Virginia and the impact of invasion by *Harmonia axyridis*. Entomological News 109: 143-151.
- Chantel, C. 1972. Additions a la faune coleopterique du Quebec. Naturaliste Canadien 99: 243-244.

- Chapin, J. B. and V. A. Brou. 1991. Harmonia axyridis (Pallas), the third species of the genus to be found in the United States (Coleoptera: Coccinellidae). Proceedings of the Entomological Society of Washington 93: 630-635.
- Day, W. H. 2005. Changes in abundance of native and introduced parasites (Hymenoptera: Braconidae), and of the target and non-target plant bug species (Hemiptera: Miridae), during two classical biological control programs in alfalfa. Biological Control 33: 368-374.
- Day, W. H., D. R. Prokrym, D. R. Ellis, and R. J. Chianese. 1994. 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. Entomological News 105: 244-256.
- Elliott, N., R. Kieckhefer, and W. Kauffman. 1996. Effects of an invading coccinellid on native coccinellids in an agricultural landscape. Oecologia 105: 537-544.
- Ellis, D. R., D. R. Prokrym, and R. G. Adams. 1999. Exotic lady beetle survey in northeastern United States: *Hippodamia variegata* and *Propylea quatuordecimpunctata* (Coleoptera: Coccinellidae). Entomological News 110: 73-84.
- Forbes, S. A. 1883. The food relations of the Carabidae and Coccinellidae. Illinois State Laboratory of Natural History Bulletin 6: 33-64.
- Gordon, R. D. 1985. The Coccinellidae (Coleoptera) of America north of Mexico. Journal of the New York Entomological Society 93: 1-912.
- Hoebeke, E. R. and A. G. Wheeler. 1996. Adventive lady beetles (Coleoptera: Coccinellidae) in the Canadian maritime provinces, with new eastern records of *Harmonia quadripunctata*. Entomological News 107: 281-290.
- Kindler, S. D., W. R. Kehr, and R. L. Ogden. 1971. Influence of pea aphids and spotted alfalfa aphids on the stand, yield of dry matter, and chemical composition of resistant and susceptible varieties of alfalfa. Journal of Economic Entomology 64: 653-657.
- Kirby, W. and W. Spence. 1860. An introduction to entomology. Longman, Green, Longman, & Roberts, Philadelphia, Pennsylvania, U.S.A. 607 pp.
- Larochelle, A. 1979. Coccinella septempunctata L. (Col: Cocc.) au Quebec: repartition, geographique, habitat et biologie. Bulletin Inventory Insects Quebec 1:68-77.
- Sailer, R. I. 1978. Our immigrant insect fauna. Bulletin of the Entomological Society of America 24: 3-11.
- Sanderson, E. D. 1900. The destructive pea louse in Delaware. Delaware Agricultural Experiment Station Bulletin 49: 14-24.
- Stephens, E. J. 2002a Apparent extirpation of *Coccinella novemnotata* in New York State: optimizing sampling methods and evaluating explanations for decline. M.S. Thesis. Cornell University. Ithaca, New York, U.S.A. 63 pp.
- Stephens, E. J. 2002b. Compilation of *Coccinella 9-notata* data collected by G. W. Angalet (USDA), 1966-1978. (Unpublished) 6 pp.
- Turnock, W. J., H. Wise, and F. O. Matheson. 2003. Abundance of some native coccinellines (Coleoptera: Coccinellidae) before and after the appearance of *Coccinella septempunctata*. Canadian Entomologist 135: 391-404.
- Wheeler, A. G. Jr. 2003. Brumoides septentrionis davisi (Leng) (Coleoptera: Coccinellidae): distribution, host-plant associations, and habitats of a seldom-collected lady beetle. Proceedings of the Entomological Society of Washington 105: 50-58.
- Wheeler, A. G. Jr. and E. R. Hoebeke. 1981. A revised distribution of *Coccinella undecimpunctata L*. in eastern and western North America. Coleopterists Bulletin 35: 213-216.
- Wheeler, A. G. Jr. and E. R. Hoebeke. 1995. Coccinella novemnotata in northeastern North America: historical occurrence and current status (Coleoptera: Coccinellidae). Proceedings of the Entomological Society of Washington 97: 701-716.
- Wheeler, A. G. Jr. and C. A. Stoops. 1996. Status and spread of the palearctic lady beetles *Hippodamia variegata* and *Propylea quatuordecimpunctata* (Coleoptera: Coccinellidae) in Pennsylvania, 1993-1995. Entomological News 107: 291-298.
- Wright, R. J. and T. A. DeVries. 2000. Species composition and relative abundance of Coccinellidae (Coleoptera) in south central Nebraska field crops. Journal of the Kansas Entomological Society 73: 103-111.