Suitability of Three Prey Species for Nearctic Populations of Coccinella septempunctata, Hippodamia variegata, and Propylea quatuordecimpunctata (Coleoptera: Coccinellidae)

JOHN J. OBRYCKI AND CANDY J. ORR

Department of Entomology, Iowa State University, Ames, Iowa 50011

J. Econ. Entomol. 83(4): 1292-1297 (1990)

ABSTRACT Coccinella septempunctata L. larvae reared at 23 ± 2°C (16:8 [L:D]) on pea aphids, Acyrthosiphon pisum (Harris), required an average of 13.1 d to complete development, a significantly faster rate of development than observed on corn leaf aphids, Rhopalosiphum maidis (Fitch) (16 d). Adult C. septempunctata from larvae reared on A. pisum were larger and weighed more than adults reared on R. maidis. Developmental times of Nearctic Hippodamia variegata Goeze and Propylea quatuordecimpunctata L., were not influenced by larval prey, but adult P. quatuordecimpunctata were heavier and larger when reared on A. pisum. First instars of the three coccinellid species tested did not feed on European corn borer eggs, Ostrinia nubilalis (Hübner) and desiccated within 3 d at 23°C. A. pisum is a highly suitable larval prey for Nearctic populations of these predators; redistribution program releases in alfalfa infested with A. pisum are appropriate. In corn, these coccinellids can develop on R. maidis, but first instars cannot utilize O. nubilalis eggs as an alternate food source.

KEY WORDS Insecta, Coccinella septempunctata, Hippodamia variegata, Propylea quatuordecimpunctata

AN UNDERSTANDING of prey suitability for introduced insect predators provides a basis for examining the potential range of predator-prey interactions in the field and interpreting results of these releases (Hagen et al. 1976). The present studies were done to quantify aspects of the predator-prey relationships for three newly established Palearctic coccinellids in North America, Coccinella septempunctata L., Hippodamia variegata (Goeze), and Propylea quatuordecimpunctata L. (Schaefer & Dysart 1988). Since 1973, C. septempunctata has rapidly expanded its range throughout eastern and central North America (Obrycki et al. 1987, Schaefer et al. 1987). By comparison, P. quatuordecimpunctata, collected in 1968 near Quebec, Canada, has dispersed less than 500 km in 20 yr (Gordon 1985, Dysart 1988). The third species, H. variegata, has only recently been discovered in eastern Canada (Gordon 1987).

These coccinellids are abundant in a wide range of Palearctic and African agroecosystems, preying upon several economically important aphid species (e.g., Chambers et al. 1983, Aalbersberg et al. 1984, Angood 1985, Honek 1985). Eurasian populations of these species are well studied (Hodek 1973), but relatively few studies have examined the biology and ecology of North American populations (e.g., Rogers et al. 1972, Obrycki & Tauber 1981, Karieva 1987, Michels & Bateman 1986).

Currently, C. septempunctata, H. variegata, and P. quatuordecimpunctata are being collected and reared for the biological control program against the Russian wheat aphid (Diuraphis noxia (Mord-

vilko)). Collections from aphid-infested cereals have been made in Turkey, France, and the USSR, in addition to redistribution of established Canadian populations, for release in regions infested by *D. noxia* in the United States (Puttler & Reed 1988, Flanders & Nelson 1989).

As part of a series of studies to document interactions of these exotic coccinellids with selected abiotic and biotic factors in the central United States (Obrycki 1989; J.J.O. & C.J.O., unpublished data), we initiated the present prey suitability tests. The objectives were to quantify the influence of three relatively common, potential prey species in the Midwest (European corn borer eggs, Ostrinia nubilalis (Hübner); corn leaf aphids, Rhopalosiphum maidis (Fitch); and pea aphids, Acyrthosiphon pisum (Harris) on larval development and survival and on adult size and weight of these three coccinellid species.

Materials and Methods

Adult C. septempunctata, H. variegata, and P. quatuordecimpunctata (2-4 generations removed from field) were obtained from the USDA-APHIS Biological Control Laboratory, Niles, Michigan, during 1987-1988. C. septempunctata originated from Georgia and Delaware; H. variegata and P. quatuordecimpunctata were reared from Montreal, Quebec, Canada, collections. Mating pairs were maintained at a photoperiod of 16:8 (L:D), 23 ± 2°C and provided with a standard diet of water, a Wheast (Qualcepts Nutrients, Minneap-

Table 1. Mean preimaginal developmental time and percentage of females and survival for C. septempunctata (C7), H. variegata (HV), and P. quatuordecimpunctata (P14) reared on two aphids at $23 \pm 2^{\circ}$ C and a photoperiod of 16:8

Cocci- nellid		Developmental times (days ± SE)							%			
	No. replicate Aphid prey		F	Instar			- Total ^b larval	Dunal	Total	T1	Survival	
species			Egg	First	Second	Third	Fourth	- i otai - iarvai	rupai	preimaginal	Females	Survivai
C7	(15, 21, 23) (19, 20, 22)	R. maidis A. pisum	3.6 3.8	3.1 3.1	2.2 2.2	2.6 2.4	8.0 5.4	16.0 ± 1.5 13.1 ± 1.4	6.0 6.3	25.7 ± 3.5 23.3 ± 3.5	54 ± 8 56 ± 9	79 ± 10 83 ± 3
HV	(22, 25, 23) (23, 22, 21)	R. maidis A. pisum	3.5 3.7	3.0 3.3	2.0 2.2	2.1 1.8	4.6 4.0	11.8 ± 2.0 11.3 ± 1.5	4.2 4.3	19.4 ± 3.3 19.3 ± 2.8	$\begin{array}{ccc} 43 \pm & 6 \\ 49 \pm & 7 \end{array}$	95 ± 3 88 ± 2
P14	(18, 23, 22) (18, 25, 20)	R. maidis A. pisum	3.6 3.4	2.6 2.6	1.9 1.8	1.7 1.9	4.2 3.3	10.4 ± 1.2 9.6 ± 1.4	5.2 5.2	19.2 ± 2.2 18.2 ± 2.5	49 ± 13 42 ± 6	90 ± 1 94 ± 4

^a Significant differences for fourth-instar developmental times between diets for each species (ANOVA, F = 9.0; df = 2, 17; P < 0.006).

olis)-honey mixture, and a daily supply of R. maidis and A. pisum. Larvae from three replications of 4-6 females (5 larvae/female) were reared individually in glass vials on either O. nubilalis eggs, R. maidis, or A. pisum at 22-24°C, at a photoperiod of 16:8 and checked daily for ecdysis. The R. maidis were reared on 'Robust' barley (Hordeum vulgare L.), and A. pisum were reared on 'Windsor' broad bean (Vicia faba L.). Both aphids were provided ad lib daily, R. maidis on leaf sections or A. pisum without plant material. The O. nubilalis used in these studies were reared on wheat germ (Lewis & Lynch 1969) using methods described by Guthrie et al. (1985). Preimaginal developmental times, survival, and the sex of emerging adults were recorded for individuals reared on each diet. Individuals were frozen 1 d after adult eclosion, weighed to the nearest milligram, and measured (mm) for overall body length and width. Data were analyzed by using analysis of variance (ANOVA) (SAS Institute 1985). Voucher specimens of the three species are deposited in the Iowa State Insect Collection, Department of Entomology, Iowa State University, Ames.

Results

European corn borer eggs are not suitable prey for larvae of C. septempunctata, H. variegata, and P. quatuordecimpunctata. No individuals survived to the second instar when provided O. nubilalis egg masses; first instars did not feed on the eggs and desiccated within 3 d. Because of this mortality on O. nubilalis eggs, the statistical analysis for diet effects was limited to A. pisum and R. maidis.

First-, second-, and third-instar developmental times of each predator were not different for the two aphid prey (Table 1). The duration of the fourth instar for each coccinellid predator was significantly longer on R. maidis than on A. pisum. This influence of aphid prey on the fourth instar was reflected in the total larval developmental time for C. septempunctata, which was significantly longer on R. maidis. (Table 1). Rearing C. septempunctata, H. variegata, or P. quatuordecimpunc-

tata on R. maidis or A. pisum did not influence the percentage of survival or sex ratio (Table 1).

No significant diet-by-sex interaction was observed for any of the three species, so adult size and weight data presented are for combined female and male values (Fig. 1 and 2). However, females of each coccinellid species reared on each prey were significantly heavier and larger than males reared on the same prey (Table 2).

Adult C. septempunctata reared on A. pisum weighed ($x \pm SD$; 0.035 \pm 0.004 g) significantly more than adults reared on R. maidis (0.022 \pm 0.004 g) (Fig. 1). C. septempunctata adults reared on A. pisum were also significantly larger (7.39) mm \times 5.74 mm) than those reared on R. maidis $(6.46 \text{ mm} \times 5.06 \text{ mm})$ (Fig. 2). The weight of H. variegata adults (0.008 ± 0.002 g) was not influenced by the two aphid diets. However, adult H. variegata were significantly larger (4.97 mm × 3.15 mm) when reared on A. pisum than those reared on R. maidis (4.52 mm × 2.87 mm). Compared with adults from a R. maidis diet, P. quatuordecimpunctata reared on A. pisum weighed more $(0.006 \pm 0.001 \text{ g } cf. \ 0.0056 \pm 0.002 \text{ g})$ and were slightly larger (4.23 mm × 3.31 mm) when reared on A. pisum than on R. maidis (4.06 mm × 3.19 mm) (Fig. 1 and 2).

Discussion

The inability of first-instar C. septempunctata, H. variegata, and P. quatuordecimpunctata to feed on O. nubilalis eggs limits the potential use of this lepidopterous species as an alternate larval food source. By comparison, 50% of P. quatuordecimpunctata in Poland completed development on Sitotroga cerealella (Oliver) eggs, and larval survival and development were enhanced when reared on a S. cerealella egg/A. pisum diet (Olszak 1986, 1988). The potential utilization of O. nubilalis eggs by adults of these three predators as an alternate food needs further investigation. Among indigenous coccinellids, adult Coleomegilla maculata De Geer are considered important O. nubilalis egg predators (Conrad 1959, Whitman 1975).

b Significant difference for total larval development of C7 between diets (ANOVA, F = 35.6; df = 2, 5; P < 0.03).

A. pisum is a highly suitable prey for North American populations of C. septempunctata, P. quatuordecimpunctata, and H. variegata. Similar results have been reported for two Palearctic populations of C. septempunctata from England (Blackman 1967) and Poland (Olszak 1988). Rearing C. septempunctata at 20°C on six aphid species, Blackman (1967) found A. pisum to be highly suitable, based upon mean larval developmental time (13.3 d), larval survival (81%), and adult weight at eclosion (0.0372 g). Similarly, 80% of C. septempunctata survived to the adult stage (mean weight = 0.0405 g) when reared on A. pisum at 20°C in Poland (Olszak 1988). Recent studies in Massachusetts showed that C. septempunctata pupae from larvae reared on A. pisum were heavier than those reared on greenbugs (Schizaphis graminum (Rondani)), R. maidis, or bird cherry-oat aphids (Rhopalosiphum padi (L.)), and that adults maintained on A. pisum reared from larvae fed A. pisum produced more eggs per female per day than adults similarly maintained and reared on either S. graminum, R. maidis, or R. padi (W. C. Kauffmann & C. P. Schwalbe, unpublished data).

Fewer studies have been done on aphid suitability for *P. quatuordecimpunctata* and *H. variegata* development and survival. Olszak (1988) reported that 67% of *P. quatuordecimpunctata* reared on *A. pisum* survived to adults (mean weight = 0.0064 g). Previously, Rogers et al. (1972) showed that survival of *P. quatuordecimpunctata* ranged from 27 to 69% when reared on several aphids associated with small grains and sunflower. By comparison, more than 90% of the *P. quatuordecimpunctata* in our study completed development on either *A. pisum* or *R. maidis*.

Hippodamia variegata from Africa required 17 d to complete development when reared on S. graminum at 25°C; larvae consumed an average of 20 aphids per day (Michels & Bateman 1986). In China, Wang et al. (1984) documented H. variegata feeding on S. graminum, Myzus persicae (Sulzer), and R. maidis and reported overall mean larval and adult consumption rates of 31 and 66 aphids per day, respectively.

Hippodamia variegata was accidentally introduced into Africa and is now the most abundant coccinellid in D. noxia-infested wheat but is also common in lucerne and uncultivated habitats (Aalbersberg et al. 1984, 1988). Similarly, C. septempunctata, P. quatuordecimpunctata, and H. variegata are abundant in aphid-infested Eurasian cereal fields but also are among the most abundant coccinellid species in potatoes, sugar beets, and alfalfa (Hodek 1973, Rautapää 1975). Although the target insect for releases of these predators in the United States is D. noxia, examination of the suitability of nontarget prey species is warranted and may be critical for the successful establishment of these predatory species.

Several nonprey-specific insect predators (generalists), including aphidophagous coccinellids, used

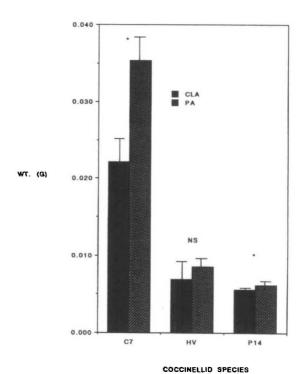


Fig. 1. Mean (+SE) weight (g) of emerging adult C. septempunctata (C7), H. variegata (HV), and P. quatuordecimpunctata (P14) reared on two aphids, R. maidis (CLA) and A. pisum (PA). * indicates significant difference between diets, P < 0.05, ANOVA. NS, not significant.

in classical biological control have not been easily established or did not result in successful biological control (Hagen 1962, Gordon 1985). Various reasons have been proposed to explain these poor results, including lack of understanding of prey specificity and potential competition for prey with existing indigenous predatory species (Thompson 1951, Hagen et al. 1976). For example, releases of C. septempunctata in the United States occurred over a 15-yr period with little apparent success. The subsequent discovery of established populations in Canada and the United States cannot be accurately traced to specific release efforts and may be a fortuitous introduction (Larochelle 1979, Schaefer et al. 1987). One of the established populations was found in a New Jersey tidal salt marshmeadow habitat, feeding upon nontarget aphid prey (Angelet & Jacques 1975). Similarly, in biological control programs directed against the Colorado potato beetle, Leptinotarsa decemlineata (Say), in Europe, releases of predatory pentatomids Perillus bioculatus (F.) and Podisus maculiventris (Say) have not resulted in permanent establishment of these predators (see Clausen 1978). Recent studies with P. maculiventris have shown not only that an understanding of prey range is required with these nonspecific predators but also that host plant feed-

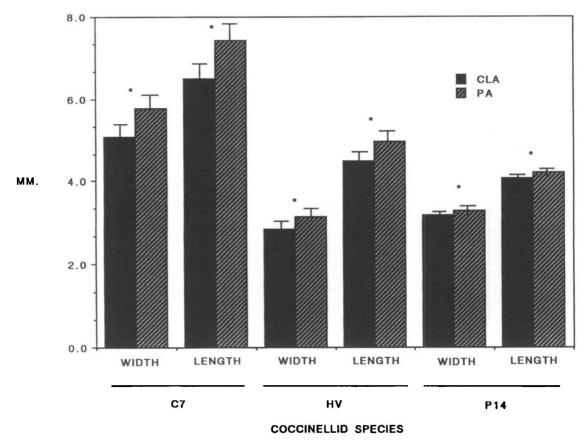


Fig. 2. Mean (+SE) length and width (mm) of adult C. septempunctata (C7), H. variegata (HV), and P. quatuordecimpunctata (P14) reared on two aphids, R. maidis (CLA) and A. pisum (PA). * indicates significant difference between diets, P < 0.05, ANOVA. NS, not significant.

ing has a significant effect on development and reproduction (Ruberson et al. 1986). Understanding the role of alternate prey and nonprey items not only improves the likelihood of permanent establishment of nonspecific predators, but is required for any subsequent manipulations of predatory species (Hagen & Hale 1974) and may provide

a rational basis for concerns regarding the ecological effect of these predatory species (e.g., Howarth 1983).

Acknowledgment

We thank R. V. Flanders and T. Burger, USDA-APHIS Biological Control Laboratory, Niles, Michigan, for adults

Table 2. Characteristics of adults of C. septempunctata (C7), H. variegata (HV), and P. quatuordecimpunctata (P14) reared on two aphids at $23 \pm 2^{\circ}$ C and a photoperiod of 16:8

Coccinellid	Sex	Aphid	Weight, g	Length, mm	Width, mm
C7	ç	A. pisum	0.0377 ± 0.003	7.65 ± 0.25	5.91 ± 0.13
		R. maidis	0.0233 ± 0.006	6.71 ± 0.11	5.19 ± 0.1
	đ	A. pisum	0.0321 ± 0.001	7.13 ± 0.3	5.56 ± 0.11
		R. maidis	0.0204 ± 0.002	6.22 ± 0.17	4.93 ± 0.05
HV	Q	A. pisum	0.0092 ± 0.001	5.16 ± 0.23	3.27 ± 0.09
		R. maidis	0.0066 ± 0.001	4.66 ± 0.04	2.98 ± 0.13
	ð	A. pisum	0.008 ± 0.001	4.78 ± 0.25	3.02 ± 0.12
		R. maidis	0.0061 ± 0.001	4.37 ± 0.15	2.75 ± 0.12
P14	Q	A. pisum	0.0067 ± 0.001	4.38 ± 0.05	3.41 ± 0.04
		R. maidis	0.006 ± 0.002	4.19 ± 0.14	3.25 ± 0.1
	ð	A. pisum	0.006 ± 0.001	4.08 ± 0.07	3.21 ± 0.02
		R. maidis	0.005 ± 0.001	3.92 ± 0.06	3.13 ± 0.02

For each species characteristic combined over the two aphid prey, females were significantly (ANOVA; P = 0.05) heavier and larger.

of the three coccinellids used in these studies. We thank R. V. Flanders and W. Kauffman, USDA-APHIS Otis Methods Development Laboratory, Massachusetts, and D. B. Orr, Iowa State University, Ames, for critically reviewing this manuscript. We thank Aaron Gabriel, Lindsay Milbrath, Margaret Lewis, Andrew Ormord, and Debra Weir for technical assistance. This work was supported in part by a USDA-APHIS cooperative agreement 12-34-41-0008. This is Journal Paper J-13570 of the Iowa Agriculture and Home Economics Experiment Station, Ames, Project 2755.

References Cited

- Aalbersberg, Y. K., M. C. Walters & N. J. van Rensburg. 1984. The status and potential of biological control studies on *Diuraphis noxia* (Aphididae), pp. 44-46. In M. C. Walters [ed.], Progress in Russian wheat aphid (*Diuraphis noxia*) Mordu. Republic of South Africa, Department of Agriculture Technical Communication 191.
- Aalbersberg, Y. K., M. C. van der Westhuizen & P. H. Hewitt. 1988. Natural enemies and their impact on Diuraphis noxia (Mordvilko) (Hemiptera: Aphididae) populations. Bull. Entomol. Res. 78: 111-120.
- Angelet, G. W. & R. L. Jacques. 1975. The establishment of Coccinella septempunctata L. in the continental United States. USDA Cooperative Economic Insect Report 25: 883-884.
- Angood, S. A. Ba-. 1985. Control of cereal aphids on wheat in People's Democratic Republic of Yemen. Insect Sci. Appli. 6: 221-225.
- Blackman, R. L. 1967. The effects of different prey on Adalia bipunctata L. and Coccinella 7-punctata L. Ann. Appl. Biol. 59: 207-219.
- Chambers, R. J., K. D. Sunderland, I. J. Wyatt & A. F. G. Dixon. 1983. The effects of predator exclusion and caging on cereal aphids in winter wheat. J. Appl. Ecol. 20: 209-224.
- Clausen, C. P. [ed.]. 1978. Introduced parasites and predators of arthropod pests and weeds: a world review. USDA Agriculture Handbook 480.
- Conrad, M. S. 1959. The spotted lady beetle, Coleomegilla maculata (DeGeer), as a predator of European corn borer eggs. J. Econ. Entomol. 52: 843-847.
- Dysart, R. J. 1988. The European lady beetle Propylea quatuordecimpunctata: new locality records for North America (Coleoptera: Coccinellidae). J. N.Y. Entomol. Soc. 96: 119–121.
- Flanders, R. V. & D. J. Nelson. 1989. Aphid biological control project: FY89 project report. USDA-APHIS Biological Control Laboratory, Niles, Mich.
- Gordon, R. D. 1985. The Coccinellidae (Coleoptera) of America north of Mexico. J. N.Y. Entomol. Soc. 93: 1-912.
- 1987. The first North American records of *Hippodamia variegata* (Goeze) (Coleoptera: Coccinellidae).

 J. N.Y. Entomol. Soc. 95: 307–309.
- Guthrie, W. D., J. C. Robbins & J. L. Jarvis. 1985.
 Ostrinia nubilalis, pp. 407-413. In P. Singh & R. F.
 Moore [eds.], Handbook of insect rearing, vol. 2. Elsevier, New York.
- Hagen, K. S. 1962. The biology and ecology of predaceous Coccinellidae. Annu. Rev. Entomol. 7: 289-326
- Hagen, K. S. & R. Hale. 1974. Increasing natural enemies through use of supplementary feeding and

- non-target prey, pp. 170–181. In F. G. Maxwell & F. A. Harris [eds.], Proceedings of Summer Institute on biological control of plant insects and diseases. University Press of Mississippi, Jackson.
- Hagen, K. S., S. Bombosch & J. A. McMurtry. 1976.
 The biology and impact of predators, pp. 93-142. In
 C. P. Huffaker & P. S. Messenger [eds.], Theory and practice of biological control. Academic, New York.
- Hodek, I. 1973. Biology of Coccinellidae. Junk, The Hague. The Netherlands.
- Honek, A. 1985. Habitat preferences of aphidophagous Coccinellids (Coleoptera). Entomophaga 30: 253–264.
- Howarth, F. 1983. Classical biocontrol: panacea or pandora's box. Proc. Hawaii Entomol. Soc. 24: 239– 244.
- Karieva, P. 1987. Habitat fragmentation and the stability of predator-prey interactions. Nature 326: 388-390
- Larochelle, A. 1979. Les Coleopteres Coccinellidae du Quebec. Cordulia Suppl. 10: 1-111.
- Lewis, L. C. & R. E. Lynch. 1969. Rearing the European corn borer, Ostrinia nubilalis (Hubner), on diets containing corn leaf and wheat germ. Iowa State J. Sci. 44: 9-14.
- Michels, C. J. & A. C. Bateman. 1986. Larval biology and life history of two imported Coccinellid (Coleoptera) predators of the greenbug (Schizaphis graminum), Hippodamia variegata Goeze and Adalia flavomaculata De Geer, at constant temperatures. Southwest. Entomol. 11: 23–30.
- Obrycki, J. J. 1989. Parasitization of native and exotic Coccinellids by *Dinocampus coccinellae* (Schrank) (Hymenoptera: Braconidae). J. Kans. Entomol. Soc. 62: 211-218.
- Obrycki, J. J. & M. J. Tauber. 1981. Phenology of three coccinellid species: thermal requirements for development. Ann. Entomol. Soc. Am. 74: 31–36.
- Obrycki, J. J., W. C. Bailey, C. R. Stoltenow, B. Puttler & C. E. Carlson. 1987. Recovery of the seven-spotted lady beetle, *Coccinella septempunctata* (Coleoptera: Coccinellidae), in Iowa and Missouri. J. Kans. Entomol. Soc. 60: 584–588.
- Olszak, R. W. 1986. Suitability of three aphid species as prey for *Propylea quatuordecimpunctata*, pp. 51-56. In I. Hodek [ed.], Ecology of aphidophaga 2. Academia, Prague.
- 1988. Voracity and development of three species of Coccinellidae preying upon different species of aphids, pp. 47-53. In E. Niemczyk & A. F. G. Dixon [eds.], Ecology and effectiveness of aphidophaga. SPB Academic Publishing, The Hague, The Netherlands.
- Puttler, B. & D. K. Reed. 1988. USDA-ARS Report on Russian wheat aphid parasites, pp. 27-30. In F. B. Peairs & S. D. Pilcher [eds.]. Proceedings of the 2nd Russian wheat aphid workshop, October 1988. Denver.
- Rautapää, J. 1975. Control of Rhopalosiphum padi (Hom., Aphididae) with Coccinella septempunctata (Col., Coccinellidae) in cages, and effect of late aphid infestation on barley yield. Ann. Agric. Fenn. 14: 231-239.
- Rogers, C. E., H. B. Jackson & R. D. Eikenbary. 1972. Voracity and survival of *Propylea 14-punctata* preying upon greenbugs. J. Econ. Entomol. 65: 1313-1316
- Ruberson, J. R., M. J. Tauber & C. A. Tauber. 1986. Plant feeding by *Podisus maculiventris* (Heteroptera: Pentatomidae): effect on survival, development

- and preoviposition period. Environ. Entomol. 15: 894-897.
- SAS Institute. 1985. SAS user's guide: statistics, version 5 ed. SAS Institute, Cary, N.C.
- Schaefer, P. W. & R. J. Dysart. 1988. Palearctic aphidophagous coccinellids in North America, pp. 99-106. In E. Niemczyk & A. F. G. Dixon [eds], Ecology and effectiveness of aphidophaga. SPB Academic Publishing. The Hague, The Netherlands. Schaefer, P. W., R. J. Dysart & H. B. Specht. 1987.
- North American distribution of Coccinella septempunctata (Coleoptera: Coccinellidae) and its mass appearance in coastal Delaware. Environ. Entomol. 16: 368–373.
- Thompson, W. R. 1951. The specificity of host relations in predaceous insects. Can. Entomol. 83: 262-
- Wang, Y. H., B. S. Liu, H. Z. Fu & L. N. Gu. 1984. Studies on the habits and bionomics of Adonia variegata (Goeze). Insect Knowledge (Kunchong Zhishi). 21: 19-22. (in Chinese).
- Whitman, R. J. 1975. Natural control of the European corn borer, Ostrinia nubilalis (Hübner), in New York. Ph.D. thesis, Cornell University, Ithaca, N.Y.

Received for publication 1 August 1989; accepted 15 November 1989