Comparative Life-History Studies of Nearctic and Palearctic Populations of *Coccinella septempunctata* (Coleoptera: Coccinellidae)

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ABSTRACT Life-history characteristics of four populations of *Coccinella septempunctata* L. were quantified and compared at 26°C and 18:6 (L:D) h on a diet of pea aphids, *Acyrthosiphon pisum* (Harris). Populations were from two locations in the United States (Iowa and Delaware) and two locations in Eurasia (France and Ukraine/Moldavia/Crimea). Large intrapopulation variation was observed in preoviposition, interoviposition, and number of days on which eggs were laid. This variation was a result of 10–35% of females entering diapause, whereas most females initiated oviposition within 12 d of eclosion and continued egg laying with interoviposition periods of <6 d. No significant differences among the four populations were detected in preoviposition, interoviposition, or number of days on which eggs were laid. In addition, preimaginal development time, sex ratio, and life table parameters, including intrinsic rates of increase and fecundity, did not differ significantly among the four populations. On the basis of the parameters measured, we conclude that these four populations of *C. septempunctata* have not undergone local adaptation that would define these populations on the basis of geographical origin.

KEY WORDS *Coccinella septempunctata*, local adaptation, geographic variation

THE SEVENSPOTTED lady beetle, *Coccinella septempunctata* L., is an introduced species permanently established in every state of the continental United States (USDA–APHIS 1991). This distribution most likely originated from three sources: (1) natural dispersal from fortuitously established populations in New Jersey and Quebec (Day et al. 1994), (2) human-assisted redistribution of populations from areas of establishment to new areas, and (3) recent releases of populations from Europe directed against the Russian wheat aphid, *Diuraphis noxia* (Mordvilko) (Homoptera: Aphididae). *C. septempunctata* is widely distributed in the Palearctic and parts of the Oriental Region, where it preys upon several economically important aphid species in various cropping systems (Hodek 1973). In many areas of North America, it became one of the dominant coccinellid species in agricultural habitats within 2–3 yr after detection (Angalet et al. 1979; Cartwright et al. 1979; Hoebeke & Wheeler 1980; Tedders & Angalet 1981; Obrycki et al. 1982, 1987; Gordon 1985; Schaefer et al. 1987; Kring & Bush 1991).

It is not known if the North American *C. septempunctata* consists of one homogeneous population or several heterogeneous populations that have independently undergone local adaptation to their new environments. The extreme case of such independent adaptation would be the formation of reproductively isolated populations (Diehl & Bush

1984, Caltagirone 1985). Previous studies of *C. septempunctata* in North America have focused on interspecific comparisons with both indigenous and introduced lady beetles (Cartwright et al. 1979, Obrycki 1989, Obrycki & Tauber 1981, Obrycki & Orr 1990, Michels & Behle 1991, Roach & Thomas 1991, Frazer & McGregor 1992, Miller & Paustian 1992). No studies have addressed intraspecific variation in Nearctic *C. septempunctata*, with the notable exception of Krafsur et al. (1992), who reported similar patterns of allozymic variation among 21 populations from Europe and North America. In our study, phenotypic variation in selected life-history traits and life-table parameters was examined among four *C. septempunctata* populations.

Materials and Methods

Representatives of two Palearctic and two Nearctic *C. septempunctata* populations were studied (Table 1). Adults collected in France and Ukraine/Moldavia/Crimea (hereafter referred to as Ukraine) were shipped to quarantine facilities at the USDA–ARS Beneficial Insects Introductions Research Laboratory (BIIRL), Newark, DE, where they were reared on pea aphids, *Acyrthosiphon pisum* (Harris), for one generation. Adults, eggs, and larvae were then shipped to the USDA–APHIS Biological Control Laboratory at Niles, MI. The bee-

Table 1. Background information on source of *C. septempunctata* populations

Population origin	Location	Latitude	Longitude	Collection date[a]	Field prey[b]	Laboratory generations[c]	Laboratory prey
Iowa	Story County Polk County	42° N	93–94° W	June, Aug. 1990 June, Aug. 1991	*A. pisum*	1	*A. pisum*
Delaware	New Castle County	39° N	75° 30–45' W	June 1990 May 1991 Dec. 1991	*A. pisum*	1	*A. pisum*
France	Alpes Meritemes	44–45° N	6– 8° E	July 1989	*D. noxia*	3–4	*S. graminum*
Ukraine/Moldavia/Crimea	Odessa/Kishinev Nikolajev/Sevastopol	44–47° N	29–34° E	May–June 1989 Oct.–Nov. 1989	*D. noxia*	3–4	*S. graminum*

[a] Names of collectors: F. Gruber for France population; S. E. Halbert, I. Kirijak, F. Gruber, and T. Poprawski for Ukraine/Moldavia population; P. W. Schaefer, S. E. Barth, C. Harris, J. Bruton, R. Cameron, and J. M. Tropp for Delaware population; M. W. Phoofolo, J. J. Obrycki, and A. M. Ormord for Iowa population.
[b] France and Ukraine/Moldavia populations were collected from wheat and barley host plants; Delaware and Iowa populations were collected from alfalfa host plants.
[c] Number of laboratory generations undergone by France and Ukraine/Moldavia populations include one generation in quarantine, during which they were fed *A. pisum.*

tles were then reared on greenbugs, *Schizaphis graminum* (Rondani), for one to two generations before adults were shipped to Ames, IA. Populations of adult *C. septempunctata* from Delaware were field collected by personnel from the USDA–ARS BIIRL at Newark, DE (Table 1), and then shipped to Ames. Adults from Iowa were collected from alfalfa fields in central Iowa (Table 1).

To ensure that inbreeding between siblings was avoided in our experiments, we maintained 10–15 pairs from each geographic population at $26 \pm 1°C$ and a photoperiod of 18:6 (L:D) h in table-top growth chambers (Percival, Boone, IA). Each pair was held in a half-pint carton (0.24 liter) covered with a piece of white organdy cloth. To supply water to the beetles, a 12-ml glass vial was filled with distilled water, plugged with cotton, and stuck through a hole punched on the side of the carton. Pairs were provided with a diet of a 1:1 mixture of honey and Wheast (Qualcepts, Minneapolis, MN) and a surplus daily supply of *A. pisum.* One egg mass from each of the 10–15 pairs was incubated at $26 \pm 1°C$ under a photoperiod of 18:6 (L:D) h; larvae were reared individually, on a diet of *A. pisum.*

Sex was determined for experimental F_1 adults for each geographic *C. septempunctata* population on the day of eclosion, and they were arranged into 10 pairs. Each member of a pair came from different parents. The mating pairs were placed individually in cages, provided with the standard diet, and maintained at $26 \pm 1°C$ and a photoperiod of 18:6 (L:D) h. In addition to the daily supply of *A. pisum,* small pieces of 'Windsor' broad bean (*Vicia faba* L.) foliage were supplied as an oviposition substrate and host for *A. pisum.* Dead aphids and old foliage were removed daily for 74 d and examined for beetle egg masses.

The preoviposition period was measured by recording the number of days from eclosion to the initiation of egg laying. Each day oviposition was observed, all eggs were counted, including the remains from cannibalized eggs. The number of days on which eggs were laid during the 74-d experimental period was determined for each female. The number of days between successive ovipositions, the interovipositional period, was recorded for each female. The oviposition period for each female is, therefore, equivalent to the interoviposition period plus the number of days on which there was oviposition. Fecundity, defined as the total number of eggs per female, was calculated for the 74-d experimental period. The percentage of females that oviposited at least once during the experiment was also recorded.

To measure preimaginal periods of development, preimaginal survival, and sex ratio for each *C. septempunctata* population, eggs were collected on the fifth day after the first oviposition from each female and thereafter at 10-d intervals. The eggs were placed in glass vials, plugged with cotton, and held at $26 \pm 1°C$ and a photoperiod of 18:6 (L:D)
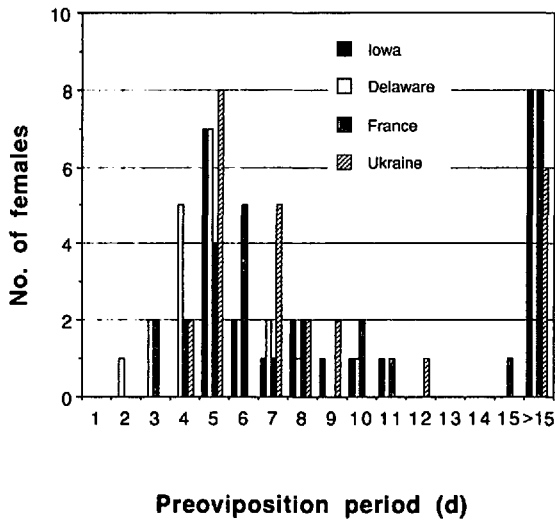
Preoviposition period (d)

Fig. 1. Frequency distribution of preoviposition periods at 26°C and a photoperiod of 18:6 (L:D) h in *C. septempunctata* populations from Iowa, Delaware, France, and Ukraine; prey was *A. pisum*.

h. Upon hatching, six first instars were chosen randomly and placed individually in glass vials. These larvae were reared at 26 ± 1°C and a photoperiod of 18:6 (L:D) h. The larvae were supplied with *A. pisum* every day. Each day the larvae were examined for molting to determine the duration of each instar and pupal stage. After adults eclosed, their sex was determined.

Estimates of the life-table parameters of the populations were calculated by using a Pascal computer program (Hulting et al. 1990). These estimates included the following: the intrinsic rate of increase (r_m), the finite rate of increase (λ), the net reproductive rate (R_0), and the mean generation time (T). A Jacknife estimate of the variance of r_m, standard errors of parameter estimates, and daily means of progeny production and survivorship were also calculated by using this program.

This study was replicated four times. Each replication consisted of 10 pairs and the rearing of up to 168 larvae for each *C. septempunctata* population.

Analysis of Data. Interpopulation variation in preoviposition and interoviposition periods, number of days on which eggs were laid, fecundity, and preimaginal development times were analyzed by the SAS general linear model procedure (SAS Institute 1985). Survival data were converted to proportions and then transformed to arcsine of the square root of these proportions before analysis of variance (ANOVA) was employed for statistical analysis. When significant differences were found, the least significant difference was used for pairwise comparisons among populations. The Student–Newman–Keuls sequential procedure was used for statistical pairwise comparisons among the r_ms for *C. septempunctata* populations (Snedecor & Cochran 1967). The significance level for all tests was set at $\alpha = 0.05$.

Results

Preoviposition periods ranged from 5 to 58 d for Iowa *C. septempunctata*, from 2 to 35 d for those from Delaware, 3–61 d for those from France, and 4–54 d for those from Ukraine. Frequency distributions of the preoviposition periods for all populations showed that the majority of females of each population (65% for Iowa; 91% for Delaware; 68% for France; 77% for Ukraine) had preoviposition periods ranging from 2 to 12 d (Fig. 1). The remaining females (except for two French females with preoviposition periods of 15 and 18 d) had preoviposition periods longer than 27 d and were assumed to be in (reproductive) diapause. Therefore, the statistical analysis for all the populations was performed on those females with a preoviposition period ≤12 d. There were no significant differences in the mean preoviposition periods among the four populations (ANOVA, $F = 1.5$; df = 3, 71; $P = 0.22$) (Table 2).

Interoviposition periods ranged from 0 (for continuously ovipositing females) to 62 d for all populations. Frequency distributions of the interoviposition periods for all populations showed bimodal pattern, with the majority of females (87.0% for Iowa population; 82.6% for Delaware population; 92.6% for France population; 79.3% for Ukraine population) having interoviposition periods ranging from 0 to 6 d (Fig. 2). Statistical analysis was performed on females with an interoviposition period ≤14 d. Interoviposition periods did not differ significantly among *C. septempunctata*

Table 2. Selected life-history traits of *C. septempunctata* populations at 26° C, 18:6 L:D h; prey was *A. pisum*

Population	Preoviposition period, d ± SEM	Inter-oviposition period, d ± SEM	No. days on which eggs were laid ± SEM	Fecundity (eggs per ♀) ± SEM	Preimaginal development time, d ± SEM	Preimaginal survival, % ± SEM[a]	Sex ratio (% ♀)[b]
Iowa	6.7 ± 0.5	4.9 ± 2.0	35 ± 4	1,357 ± 184	14.6 ± 0.2	92.9 ± 3.1a	52
Delaware	5.1 ± 0.4	6.4 ± 2.7	44 ± 4	1,563 ± 194	14.3 ± 0.3	89.8 ± 2.8ab	50
France	6.2 ± 0.5	4.3 ± 1.9	37 ± 3	1,712 ± 188	14.9 ± 0.2	82.3 ± 3.8bc	47
Ukraine/Moldavia	6.4 ± 0.4	6.8 ± 2.2	33 ± 3	1,172 ± 204	14.4 ± 0.2	78.9 ± 3.8c	55

[a] Means followed by the same letter are not significantly different ($P = 0.05$, least significant difference test).
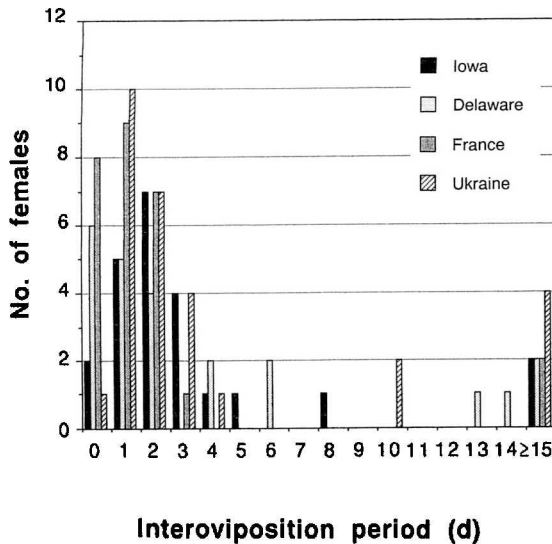[b] All other traits were not significantly different among populations.

Fig. 2. Frequency distribution of interoviposition periods at 26°C and a photoperiod of 18:6 (L:D) h in *C. septempunctata* populations from Iowa, Delaware, France, and Ukraine; prey was *A. pisum*.

populations (ANOVA, $F = 0.25$; df = 3, 71; $P = 0.86$) (Table 2).

The number of days on which eggs were laid did not differ significantly among the populations, although the differences were close to the 0.05 significance level (ANOVA, $F = 2.65$; df = 3, 71; $P = 0.056$) (Table 2). The range of the number of days on which eggs were laid was 1–67 d for Iowa *C. septempunctata*, 4–69 d for Delaware, and 1–66 d for both French and Ukraine *C. septempunctata*.

The total number of eggs per female (fecundity) did not differ significantly among the *C. septempunctata* populations (ANOVA, $F = 1.06$; df = 3, 71; $P = 0.37$). The females that had short preoviposition periods (≤ 12 d) and short interoviposition periods (≤ 6 d) had higher fecundities than females with either long preoviposition periods (>12 d) or long interoviposition periods (>6 d). However, a small proportion of females with either long preoviposition periods or long interoviposition periods oviposited several large egg masses (>60 eggs per mass) after 6–7 wk without ovipositing.

During the oviposition period, rates of oviposition and the proportion of ovipositing females in the four populations fluctuated over time (Fig. 3 A–D). These fluctuations are attributable to large intrapopulation variation in preoviposition and interoviposition periods. There was also large variation in the daily oviposition rates, which ranged from 0 to 170 eggs per female (Fig. 4). The most frequent daily oviposition rates were between 10 and 60 eggs per day per female (75.4% for Iowa females; 71.2% for Delaware females; 71.4% for French females; 75.0% for Ukraine females) (Fig. 4).
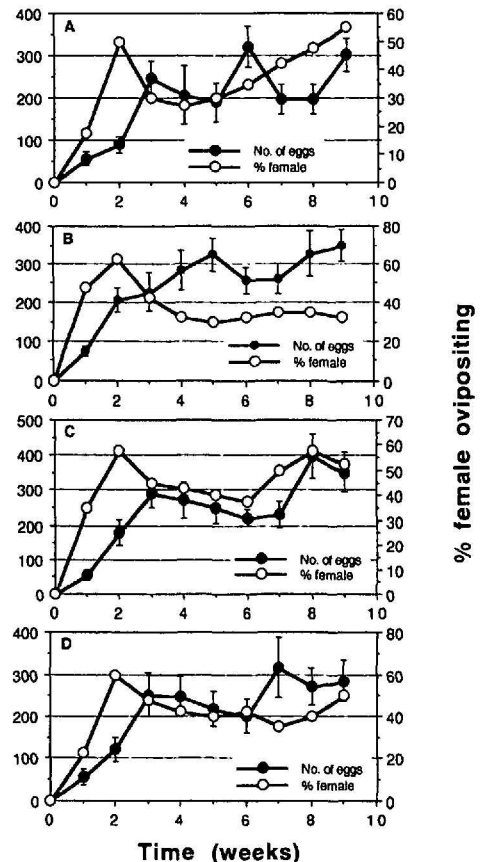

Fig. 3. Oviposition pattern in populations of *C. septempunctata* at 26°C and a photoperiod of 18:6 (L:D) h; prey was *A. pisum*. (A) Iowa. (B) Delaware. (C) France. (D) Ukraine.

The preimaginal development times did not vary significantly among the populations (ANOVA, $F = 0.47$; df = 3, 59; $P = 0.70$). At 26°C, the four populations required ≈14 d to develop from egg to adult stage (Table 2). The percentage survival of the immature stages ranged from 79 to 93% in the four populations and showed significant differences (ANOVA, $F = 3.74$; df = 3, 59; $P = 0.0158$) (Table 2). The cause of these differences in immature survival could be the different number of generations spent by each population in the laboratory (Table 1). The survival of early instars may be the first life-history trait that is affected by laboratory rearing. The sex ratio did not vary significantly among the populations (ANOVA, $F = 0.97$; df = 3, 59; $P = 0.41$) (Table 2).

The Student–Newman–Keuls test showed no significant differences in the intrinsic rate of increase ($Q = 2.12$, df = 23, $P > 0.05$) or the net reproductive rate ($Q = 0.83$, df = 23, $P > 0.05$) among the populations. The intrinsic rate of increase ranged from 0.17 ± 0.02 per female per day for the Iowa population to 0.20 ± 0.01 per female per day for the Delaware beetles (Table 3).

Table 3. Estimates of life table parameters for four representative *C. septempunctata* populations at 26°C, 18:6 (L:D) h; prey was *A. pisum*

Population	$r_m \pm SE$	$R_0 \pm SE$	T (d)	λ (d^{-1})	No. of ♀♀
Iowa	0.17 ± 0.02	559.6 ± 86.0	37.2	1.2	25
Delaware	0.20 ± 0.01	663.9 ± 91.0	31.9	1.2	23
France	0.19 ± 0.02	567.6 ± 76.5	34.0	1.2	30
Ukraine/Moldavia	0.18 ± 0.01	563.5 ± 111.9	35.4	1.2	25

The finite rate of increase for all the populations was ≈1.2 individuals per day.

Discussion

The four populations of *C. septempunctata* studied did not show significant differences in their preoviposition periods when maintained at 26°C and a photoperiod of 18:6 (L:D) h. These preoviposition periods compare closely with those of a Czech *C. septempunctata* population (9–52 d) maintained at 20–24.5°C and a photoperiod of 18:6 (L:D) h (Hodek & Ruzicka 1979) and a Finnish *C. septempunctata* population (5–12 d) maintained at 22–26°C and a photoperiod of 18:6 (L:D) h (Hamalainen 1976). Results from these three studies suggest no difference in preoviposition periods among *C. septempunctata* populations from different geographic regions.

Within each population, *C. septempunctata* females exhibited a consistent bimodal pattern in the preoviposition period: one group (65–90%) had short and another group (10–35%) had long preoviposition periods. Delayed oviposition probably reflects an inherent occurrence of reproductive diapause even under conditions that are favorable for reproduction (26°C, a photoperiod of 18:6 [L:D] h, and unlimited diet). Similar variation has been observed by other researchers. For example, 20% of the reproductive females of *C. septem-*

No. of females ovipositing

Fig. 4. Frequency distributions of daily oviposition rates of four *C. septempunctata* populations.

punctata from the Czech Republic had very long preoviposition periods (>14 d), whereas the majority (80%) of the reproductive females laid eggs within 14 d (Hodek & Ruzicka 1979). In a related study (Phoofolo et al. 1995), we also found that only 60–70% of females underwent ovarian development at five constant temperatures. The rest of the females had undeveloped ovaries similar to those of newly eclosed or diapausing (overwintering) females. A possible laboratory artifact could be a second explanation for this pattern. For example, constant warm temperatures and a photoperiod of 18:6 (L:D) h may not be optimal for all females. Females with long interoviposition and fewer number of days on which eggs were laid could be explained similarly. Furthermore, the percentage of females that laid eggs in each *C. septempunctata* population, although fluctuating over time, was relatively low, ranging from 30 to 60% (Fig. 3 A–D).

If this large range of intrapopulation variation in life-history traits associated with fecundity (e.g., preoviposition and interoviposition periods, proportion of females ovipositing, daily oviposition rates, and fecundity) is expressed in nature, it may reflect one of the factors responsible for the widespread occurrence of *C. septempunctata*. We propose that occurrence of phenotypic variation in *C. septempunctata* life-history traits may be evidence of either genetically based bet-hedging or phenotypic plasticity or a combination of these strategies. Bet-hedging strategies involve production of offspring with genetically based differences in phenotypes (e.g., for *C. septempunctata*, differences among individual females in the ability to initiate reproduction without delay). This concept was first developed by Cohen (1966) using the example of seed dormancy. Cooper & Kaplan (1982) and Kaplan & Cooper (1984) referred to this as an adaptive coin-flipping strategy, whereas Seger & Brockmann (1987) and Philippi & Seger (1989) used an analogy of "don't put all your eggs in one basket" to explain this type of adaptive strategy. Bet-hedging strategies in seasonal reproduction also have been documented in *Chrysoperla carnea* (Stephens) (Tauber & Tauber 1986, 1992, 1993).

Phenotypic plasticity is defined as the variation in the phenotypic expression of a trait induced by environmental conditions (West-Eberhard 1989, Scheiner 1993). The importance of phenotypic plasticity includes development of alternative adaptations, which West-Eberhard (1986) defined as
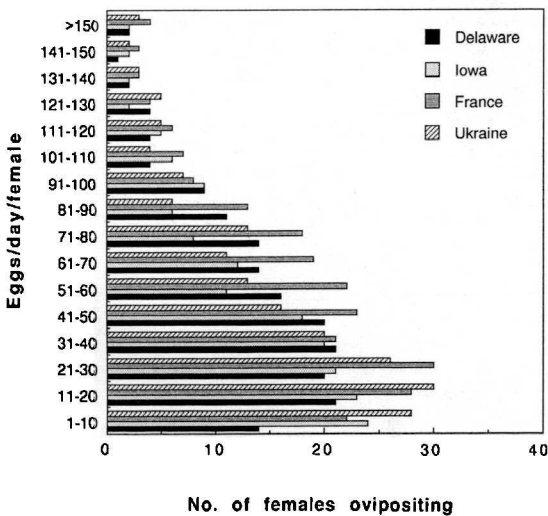
"different adaptive phenotypes maintained in the same life stage and the same population but not necessarily simultaneously expressed in the same individual." The effect of such alternative adaptations is formation of contrasting phenotypic character sets that result from the same genotype. For example, *C. septempunctata* females responded differently to the experimental conditions in this study: one category of individuals became reproductively active (nondiapausing females) and the second category entered reproductive diapause. Experiments on *C. septempunctata* in central Europe indicated that it is indeed an ecologically variable species, particularly in its response to photoperiod (Hodek & Cerkasov 1960, 1961; Hodek 1966, 1973; Hodek & Ruzicka 1979). In those experiments, as in our study, researchers observed both diapausing and reproducing (nondiapausing) females despite optimal conditions for reproduction and aversion of diapause (i.e., excess prey, long photoperiods [16–18 h light], suitable temperature [20–25°C] and relative humidity [50–70%]). Hodek (1966) concluded that this pattern reflected the occurrence of "a mixture of univoltine and multivoltine strains," whereby the nonovipositing females (and those with long preoviposition periods) experience obligatory diapause whereas reproducing females could express facultative diapause.

The release of *C. septempunctata* in North America does not represent a typical biological control program in that there was no particular target pest species for its introduction and its establishment was largely fortuitous. However, its widespread occurrence in North America presents opportunities for investigating factors that contribute to the invasiveness of colonizing species. Such factors commonly may be found in other species and should therefore be considered in future classical biological control programs, because of their potential to increase invasion rates. For example, from our study we conclude that large variation in characters that contribute to fitness, such as fecundity and the preoviposition period, whether caused by bet-hedging or phenotypic plasticity (or both), may contribute to the widespread occurrence of *C. septempunctata*. De Wilde & Hsiao (1981) also considered large variation (e.g., 40% females entered diapause, 46.6% with normal oviposition [no diapause], 2.7% with <15 eggs and no diapause, 6.6% with no eggs and no diapause, and 2.7% died within 15 d of emergence) in the response of *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae) to long photoperiod (18 h light) and 25°C to be one of the factors contributing to the invasiveness of that species.

The results of our study show that four North American and Eurasian populations of *C. septempunctata* do not differ in several life-history characteristics. They also do not appear to differ from other Eurasian (Czech and Finnish) populations. On the basis of these results, it can be concluded that this species has not undergone observable lo-cal adaptation that can define populations on the basis of geographical origin. This study supports the finding by Krafsur et al. (1992) of similar patterns of allozymic variation among representatives of numerous Palearctic and Nearctic *C. septempunctata* populations.

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