Demographic analysis of reproduction in Nearctic and Palearctic populations of *Coccinella septempunctata* and *Propylea quatuordecimpunctata*

Mpho W. PHOOFOLO[1] and John J. OBRYCKI*
*Department of Entomology, Iowa State University, Ames, Iowa 50011, USA; [1]current address: Department of Biology, National University of Lesotho, Lesotho; *author for correspondence (e-mail: jobrycki@iastate.edu)*

Abstract. *Coccinella septempunctata* and *Propylea quatuordecimpunctata* in North America have documented invasive capacity. Studies are needed to identify relevant life-history parameters responsible for their successful spatial spread. This study is a detailed analysis of phenotypic variation in reproductive traits of several Nearctic and Palearctic populations of these two coccinellid species. From 47 to 61% of *C. septempunctata* females laid their first batch of eggs within the first two weeks of their adult life. Within *P. quatuordecimpunctata* populations, 56 to 83% of females initiated oviposition within 2 weeks. The remaining females either had preoviposition periods >2 weeks or never laid eggs during a 60-day observation period. Analysis of daily fecundity revealed differences in oviposition strategies among females within each population. Repeatability estimates of daily parity for *C. septempunctata* populations were 0.32 for Iowa (USA), 0.35 for Delaware (USA), 0.28 for France, and 0.33 for Ukraine. Repeatability estimates for *P. quatuordecimpunctata* populations were 0.35 for Canada, 0.25 for France, and 0.33 for Turkey. The within-female component accounted for most of the variation in daily parity; this was due to female variability in their daily oviposition rates.

Key words: fecundity, lady beetles, parity, preoviposition period, repeatability

Introduction

Reproductive capacity is an ecological trait considered by ecologists to be a crucial factor governing the ability of exotic species to successfully invade new habitats (Crawley, 1986; Ehrlich, 1986; Roy, 1990). But, when assessing the invasive potential of species on the basis of their reproductive capacity, the focus is on measures of central tendency such as the intrinsic rate of increase, whereas heterogeneity among individuals is ignored (Bennett, 1987). For example, species or populations with high intrinsic rate of increase are considered to have higher invasive potential (MacArthur and Wilson, 1967; Crawley, 1986); but similar to other traits of an ideal biological invader, there

is little evidence to indicate that this prediction applies to all species (Parsons, 1983; Lawton and Brown, 1986; Ehrlich, 1986; Roy, 1990; Lodge, 1993). The analysis of heterogeneity among individuals needs greater consideration in invasion ecology, because natural selection, which drives evolutionary change and hence adaptation to novel environmental conditions, acts primarily on phenotypes.

Our objective in this paper is to analyze phenotypic variation in reproductive traits of Nearctic and Palearctic populations of aphidophagous coccinellid species, *Coccinella septempunctata* L. and *Propylea quatuordecimpunctata* L. (Coleoptera: Coccinellidae). Both species are indigenous to the Palearctic region, where they are widely distributed (Hodek, 1973), but they have also established in the Nearctic region (Day et al., 1994). Since its detection in North America in 1973, *C. septempunctata* has expanded its distribution across most of the continental USA and become one of the dominant coccinellids in agricultural habitats (Day et al., 1994; Elliott et al., 1996; Obrycki and Kring, 1998). The first detection of *P. quatuordecimpunctata* in North America was in 1968 in Quebec, and it has since expanded its distribution southward (Day et al., 1994). The sources of the original populations of both species that first established in North America are not known, but it is presumed that the first establishments of both species were fortuitous (Obrycki and Kring, 1998).

The invasive ability shown by these coccinellids in North America has raised several questions. Because they prey on several aphid species that are crop pests, applied ecologists may view their widespread occurrence as economically important. This view led to many human-assisted redistribution attempts of these species, particularly against the Russian wheat aphid, *Diuraphis noxia* Mordvilko (Flanders et al., 1991). However, their invasiveness and polyphagy has raised concerns about their role in displacement of native aphidophagous coccinellid species (Elliott et al., 1996; Obrycki et al., 1998a, b, 1999). We have previously reported the results of comparative studies on several life-history characteristics of selected geographic populations of these two species (Obrycki et al., 1993; Phoofolo and Obrycki, 1995). Comparisons, however, were based on averages of the life-history traits, which do not account for the heterogeneity in reproductive characteristics found within each geographic population.

Materials and methods

Sources of populations

We studied individuals of two Palearctic and Nearctic *C. septempunctata* populations and two Palearctic and one Nearctic *P. quatuordecimpunctata* populations. Palearctic adult *C. septempunctata* were originally collected in 1989 from France and Ukraine. These adults were shipped to quarantine facilities at the USDA-ARS BIIR Laboratory, Newark, DE, USA where they were reared on pea aphids for one generation. Adults, eggs, and larvae were then shipped to the USDA-APHIS Biological Control Laboratory at Niles, MI. The beetles were then reared on greenbugs for one to two generations before adults were shipped to Ames, IA. Nearctic adult *C. septempunctata* from Delaware were field-collected by personnel from the USDA-ARS BIIRL at Newark, DE and then shipped to Ames during 1990–1991. Adults from Iowa were collected from alfalfa fields in central Iowa during 1990–1991.

Palearctic adult *P. quatuordecimpunctata* were originally collected from Turkey and France in 1989. Nearctic adult *P. quatuordecimpunctata* were collected from Quebec, Canada in 1989. These beetles were shipped to quarantine facilities at the USDA-ARS BIIRL, Newark, DE, where they were reared on pea aphids for one generation. Adults, eggs, and larvae were then shipped to USDA-APHIS Biological Control Laboratory at Niles, MI. There, the beetles were reared on greenbugs for one to two generations before adults were shipped to Ames, IA.

Experimental procedures

Experimental F1 adults for each geographic population for each coccinellid species were sexed on the day of eclosion and arranged into 40 pairs. Each member of a pair came from different parents. The mating pairs were individually held in a half-pint carton (0.24 1) 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 in the side of the carton. Pairs were provided with a diet of a 1:1 mixture of honey and Wheast$^{®}$ (Qualcepts Co., Minneapolis, MN) and a surplus daily supply of *A. pisum*. Pairs were maintained at $26 \pm 1 \,°C$ and a photoperiod of L18:D6 h for *C. septempunctata* and L16:D8 for *P. quatuordecimpunctata*.

Daily fecundity, defined as the number of eggs oviposited per female per day, was determined by counting all eggs including the remains from cannibalized eggs over the first 60 days of the adult life span. We chose a 60-d observation period to represent the major reproductive period (late spring) for these two species in northern temperate regions.

Data collection and analysis

Age at reproductive maturity
Reproductive maturity was assessed as the age of first reproduction, i.e. age of female when it lays its first batch of eggs. Variation in reproductive maturity was evaluated by determining frequency distributions of preoviposition periods among females. Preoviposition period is defined as the number of days from adult eclosion to the day before the first day of egg-laying.

Daily parity classes
The daily parity classes provide frequency distributions of daily fecundity in terms of the fraction of the female cohort whose daily fecundity falls into one of several fecundity classes (Carey et al., 1988; Carey, 1993). The daily fecundity classes used were 0 eggs, 1–29 eggs, 30–59 eggs, and ≥60 eggs. Daily fecundity was analyzed to determine the consistency of oviposition rates. The classes were selected on the basis of the relationship between number of ovarioles and egg production rates in aphidophagous coccinellids (Stewart et al., 1991a). Stewart et al. (1991a) found a linear relationship between the number of ovarioles and clutch size in 11 coccinellid species, including *C. septempunctata* and *P. quatuordecimpunctata*, described by Equation (1):

$$\text{Clutch size} = 0.54\,\text{Ovariole number} - 2.2. \tag{1}$$

The number of ovarioles is reported to range from 80–94 in *C. septempunctata* and 20–28 in *P. quatuordecimpunctata* (Iperti, 1966a). Based on the relationship in Equation (1), the daily fecundity can range from zero (i.e. no oviposition) to a (variable) number that is a multiple of clutch size, depending on how many clutches a female can lay per day. Females of both species are capable of laying >1 clutch per day (Evans and Dixon, 1986; Stewart et al., 1991b). We also know that both species have asynchronous ovariole development, i.e. not every ovariole produces eggs at the same time (Phoofolo et al, 1995).

Cumulative parity classes
This method calculates frequency of cumulative parity classes that express the fraction of the cohort whose cumulative total egg production falls into one of several classes. Cumulative parity shows the longer term consistency in egg production among females as a function of age (Carey, 1993). For example, there may be a proportion of the female cohort that does not lay eggs. Cumulative parity analysis shows how and to what extent this proportion changes as a function of the age of the females. We used the following cumulative parity

classes: 0 eggs, 1–100 eggs, 101–500 eggs, 501–1000 eggs, 1001–1500 eggs, and >1500 eggs. These classes were based upon previously published total fecundity estimates for the two species (Hodek, 1973).

Repeatability of parity

The temporal repetition of a trait allows its total phenotypic variance (V_P) to be partitioned into a within-individual and among-individuals components. Whereas the within-individual component arises solely from temporary environmental effects between successive measurements. (V_{Es}), the among-individuals variance constitutes both a genotypic (V_G) and general environmental (V_{Eg}) variance (Falconer, 1989). Repeatability, the intraclass correlation coefficient, indicates the proportion of total variation in a trait that is due to differences among individuals (Falconer, 1989). It is based on repeated measurements of the trait within the same individuals followed by a one-way analysis of variance. Repeatability, R, is defined as:

$$R = (V_G + V_{Eg})/V_P. \qquad (2)$$

The variance components used in calculating repeatability are estimated from the analysis of variance as explained by Lessels and Boag (1987). We calculated repeatability of daily parity from repeated measurements of egg production of *C. septempunctata* and *P. quatuordecimpunctata* females.

Results

Reproductive maturity

The mean preoviposition periods alone (Table 1) do not show how variable this trait is. However, the range and frequency of preoviposition periods (Figure 1) shows that, whereas most *C. septempunctata* females in all four populations laid the first batch of eggs within the first two weeks of their adult life (46.9% from Iowa, 60.0% from Delaware, 54.3% from France, and 60.6% from Ukraine), some females had preoviposition periods of >2 weeks (Iowa 25.0%, Delaware 11.4%, France 25.7%, and Ukraine 18.2%). We also found that 28.1% of females from Iowa, 28.6% from Delaware, 20.0% from France, and 21.1% from Ukraine did not lay eggs during the 60-d experimental period.

Similarly for *P. quatuordecimpunctata*, we found that, whereas most females reached reproductive maturity by their second week of adult life (83.3% from Canada, 80.0% from France, and 56.4% from Turkey) (Figure 2), some females had preoviposition periods of >2 weeks (Canada 16.7%,

Table 1. Average oviposition rates of geographic populations of *Coccinella septempunctata* and *Propylea quatuordecimpunctata*

Species	Population	Preoviposition period,		Total eggs per female	Eggs per female per day	
		d	(SD)		per day	(SEM)
C. septempunctata	Iowa	20.7	(19.5)	861	11.9	(15.6)
C. septempunctata	Delaware	13.7	(20.1)	863	16.0	(17.8)
C. septempunctata	France	16.0	(17.1)	1032	19.0	(18.9)
C. septempunctata	Ukraine	15.3	(16.4)	891	17.2	(18.7)
P. quatuordecimpunctata	France	8.6	(8.1)	625	11.9	(5.9)
P. quatuordecimpunctata	Turkey	7.0	(4.0)	532	9.3	(6.7)
P. quatuordecimpunctata	Canada	17.2	(13.8)	441	7.0	(6.0)

France 8.6%, and Turkey 38.5%). However, unlike *C. septempunctata* populations, all *P. quatuordecimpunctata* females from Canada laid eggs by the end of the experimental period and only 11.4% and 5.1% of females from France and Turkey, respectively, did not lay eggs in 60 days.

Daily parity

There were no significant differences among populations of each species in mean daily fecundity per female (*C. septempunctata* ANOVA, F = 1.30; df = 3, 147; $P = 0.28$; *P. quatuordecimpunctata* ANOVA, F = 2.85; df = 2, 110; $P = 0.10$) (Table 1). Frequency distributions show that there is considerable variation in daily parity for both species (Figures 3 and 4). For example, on day 20, 73.7% of the cohort of *C. septempunctata* females from Iowa did not lay eggs, 13.2% laid 1–29 eggs, 5.3% laid 30–59 eggs, and 7.9% laid >59 eggs. Females of *P. quatuordecimpunctata* also had variation in daily parity as shown by the population from France on day 20, where 25.0% did not lay eggs, 63.9% laid 1–29 eggs, and 8.3% laid 30–59 eggs. The >59 eggs daily parity class was not observed in any *P. quatuordecimpunctata* population. This is due to their smaller body size and fewer ovarioles relative to *C. septempunctata*. The other factor that contributes to variation in daily parity is the occurrence of a large proportion of females that belonged to the null-parity class (females that did not lay eggs) for all ages (Figures 3 and 4).

Both the reproductively immature and mature females formed the null-parity class. In both species, most reproductively mature females did not lay eggs daily (Figures 5 and 6). For *C. septempunctata*, the percentage of days on which a mature female laid at least one egg ranged from 1.9 to 96.4%
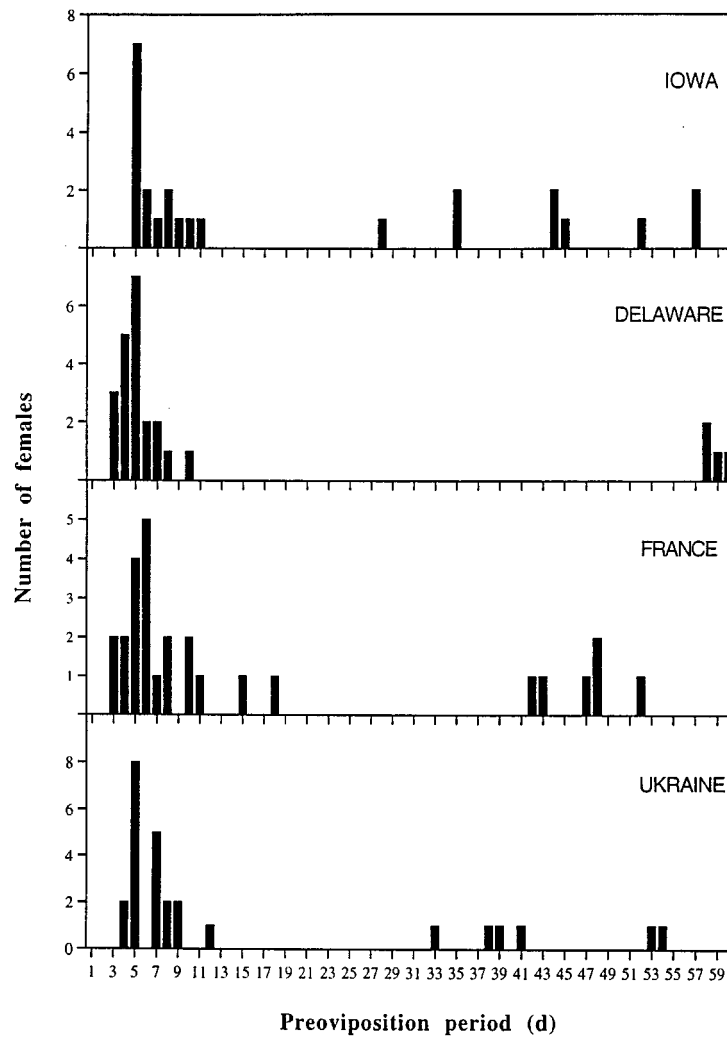
Figure 1. Frequency distributions of preoviposition periods in *C. septempunctata* populations from Iowa, Delaware, France, and Ukraine.

among Iowa females, 7.4 to 100% among Delaware females, and 1.9 to 100% among females from France and Ukraine. For *P. quatuordecimpunctata* the percentage of days on which a reproductively mature female laid at least one egg ranged from 19.6 to 100% among French females, 15.9 to 98.2% among Turkish females, and 2.3 to 100% among females from Canada.
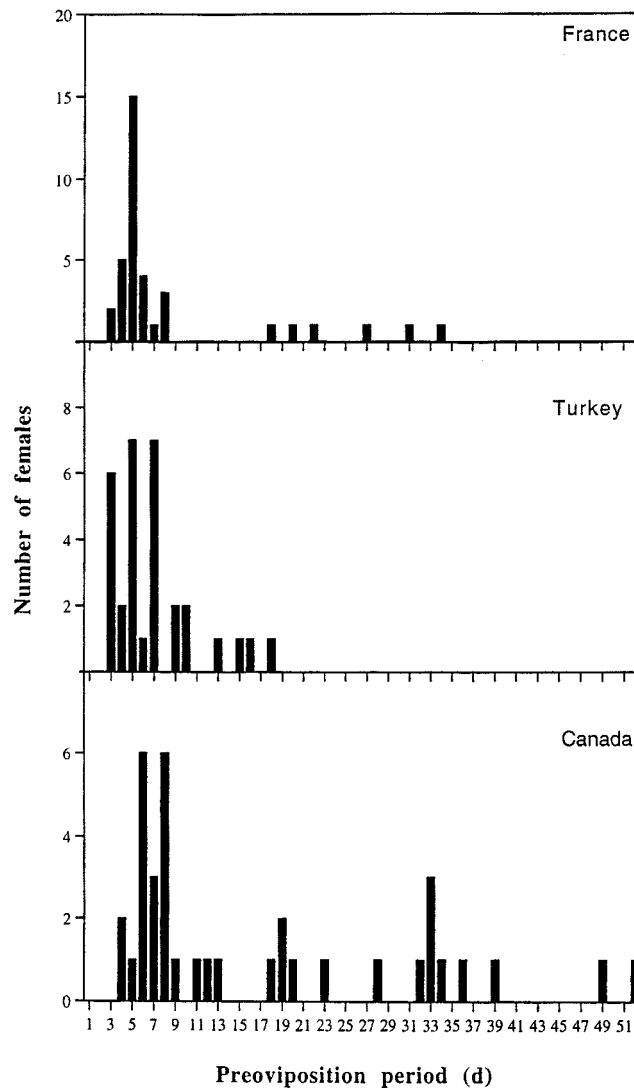
Figure 2. Frequency distributions of preoviposition periods in *P. quatuordecimpunctata* populations from France, Turkey, and Canada.

Cumulative parity

There were wide ranges in oviposition rates of both species as reflected by the occurrence of different cumulative parity classes (Figures 7 and 8). For example, in age class 7, out of the cohort of 38 *C. septempunctata* females from Iowa, 68.4% had not laid eggs, 23.7% had laid between 1–100 eggs, and the remaining 7.9% had laid 101–500 eggs (Figure 7A). By age class 35,
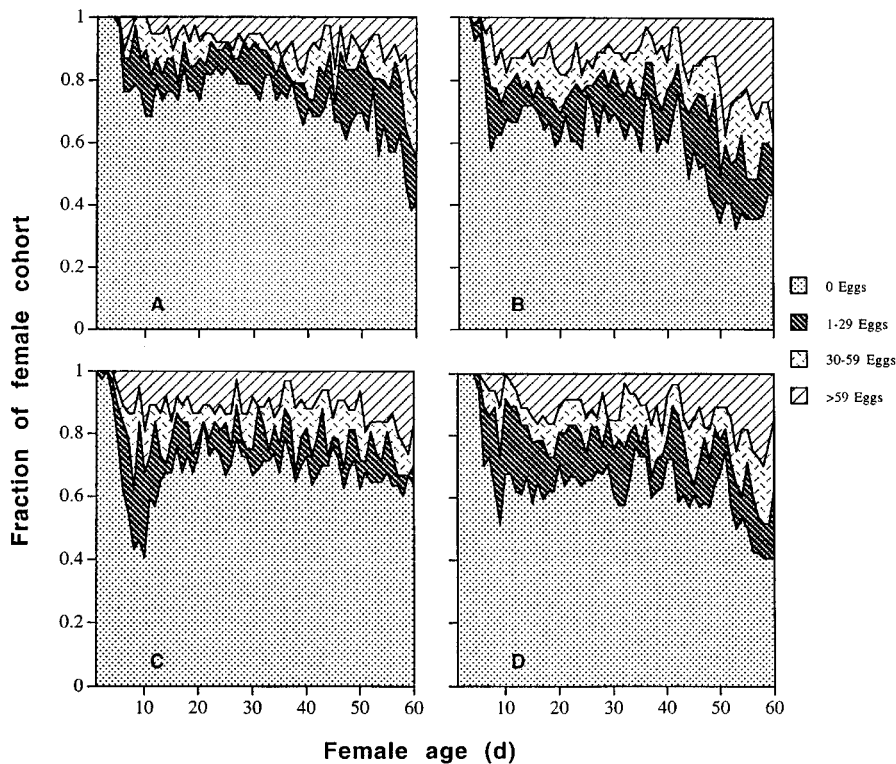
Figure 3. Fraction of females in *C. septempunctata* populations which had laid 0 eggs, 1–29 eggs, 30–59 eggs, and >59 eggs by age (daily parity). A, Iowa; B, Delaware; C, France; D, Ukraine.

44.7% of the 38 Iowa females still had not laid eggs, whereas 26.3% had laid 1–100 eggs, 10.5% and laid 101–500 eggs, 2.6% had laid 501–1000 eggs, 10.5% had laid 1001–1500 eggs, and the remaining 5.3% had laid >1500 eggs. The spread in oviposition rates among females of the other three *C. septempunctata* populations was such that by the end of the first week of adult life, only the first 3 cumulative parity classes were represented, whereas by the end of the 5th week all the parity classes were represented (Figure 7B–D). Unlike *C. septempunctata*, there were no *P. quatuordecimpunctata* females with a cumulative fecundity of >1500 eggs (Figure 8), which is a consequence of their smaller body size. Also, *P. quatuordecimpunctata* populations had fewer females in the nulliparous class compared to those of the *C. septempunctata* populations (Figures 7 and 8). The average total fecundities of the populations within each species, which did not differ significantly (*C. septempunctata* ANOVA, F = 0.82; df = 3, 147; *P* = 0.49; *P. quatuordecim-*
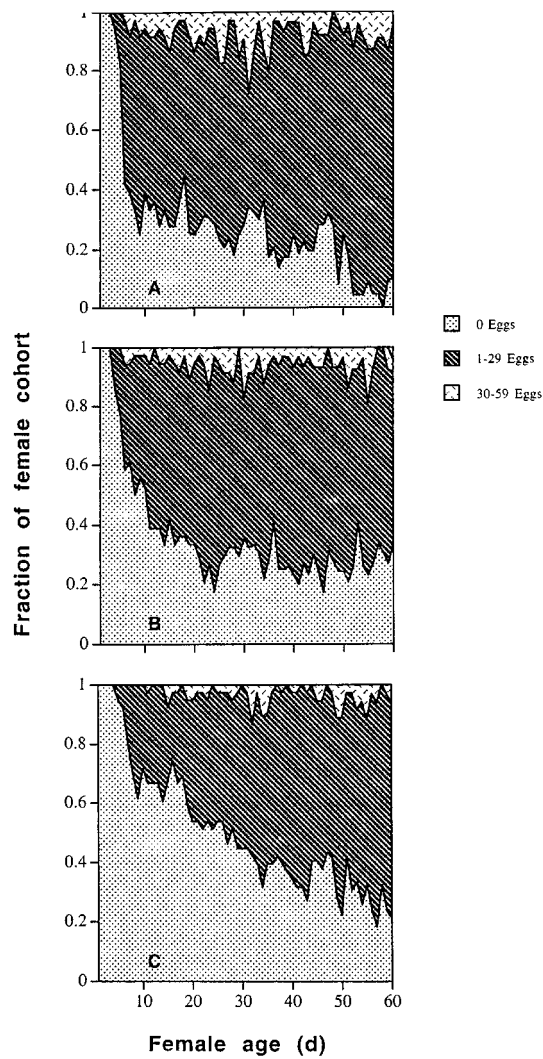
Figure 4. Fraction of females in *P. quatuordecimpunctata* populations which had laid 0 eggs, 1–29 eggs, and 30–59 eggs by age (daily parity). A, France; B, Turkey; C, Canada.

punctata ANOVA, F = 2.22; df = 2, 110; *P* = 0.11) (Table 1), do not show the variation in parity seen in Figures 7 and 8.

Repeatability of daily parity

For *C. septempunctata* populations, the within-female components of variation were larger than the among-female components (Table 2). Differences among individuals accounted for 32% of the total phenotypic variance in
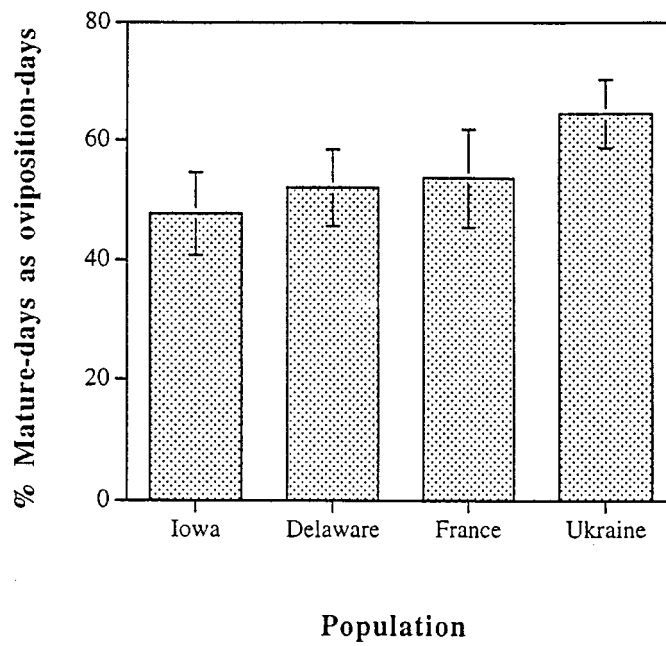
Figure 5. Percent of all days in which reproductively mature *C. septempunctata* females laid at least one egg.
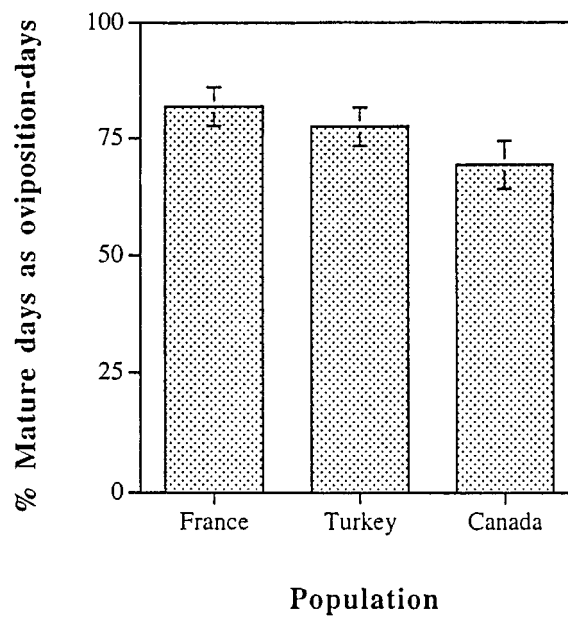

Figure 6. Percent of all days in which reproductively mature *P. quatuordecimpunctata* females laid at least one egg.
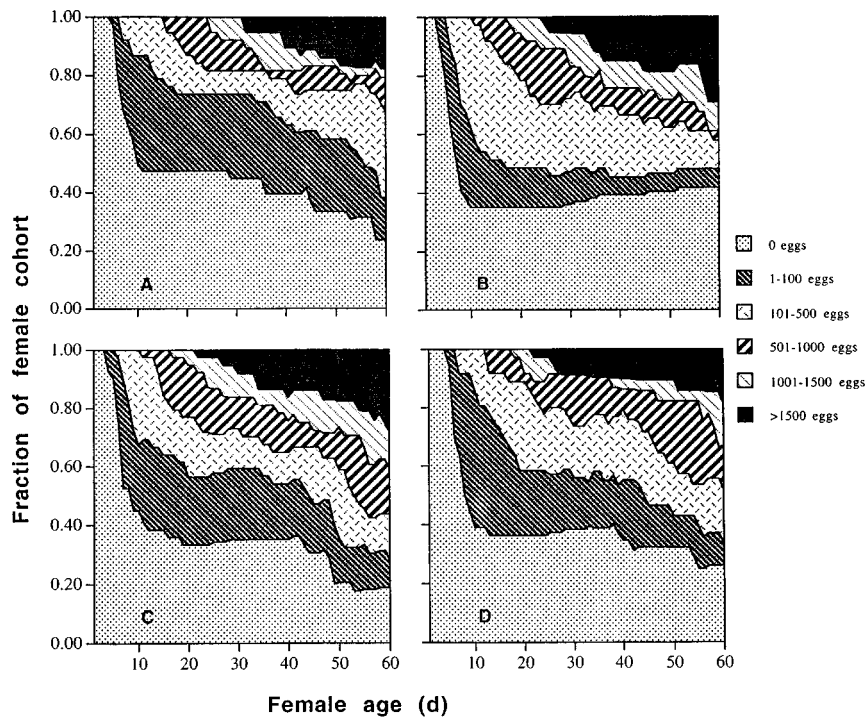
Figure 7. Fraction of females in *C. septempunctata* populations that had laid a cumulative total of 0 eggs, 1–100 eggs, 101–500 eggs, 501–1000 eggs, 1001–1500 eggs, and >1500 eggs by age (cumulative parity). A, Iowa; B, Delaware; C, France; D, Ukraine.

daily parity of Iowa females, 35% of the daily parity variance of Delaware females, 28% of the French females, and 33% of the Ukrainian females (Table 2). Similar to *C. septempunctata*, partitioning of daily parity variance indicated that for all *P. quatuordecimpunctata* populations, intra-female variance was larger than the variance resulting from differences among females (Table 2). Inter-female variance accounted for 25% of the total phenotypic variance in the daily parity of the French population, 33% of the daily parity variance of the population from Turkey, and 35% of the variance within the population from Canada (Table 2). From equation 2 it can be seen that the inter-female variation may reflect genetic differences (V_G), differences due to permanent environmental influences (V_{Eg}), or both.

The within-female variance in daily parity accounted for $\geq 65\%$ of the total variance for all populations of the two species (Table 2). These large within-female variances are due to high inconsistencies displayed by females in the number of eggs laid per day. That is, the differences in the number of eggs laid by a female each day were larger than the differences among females in their
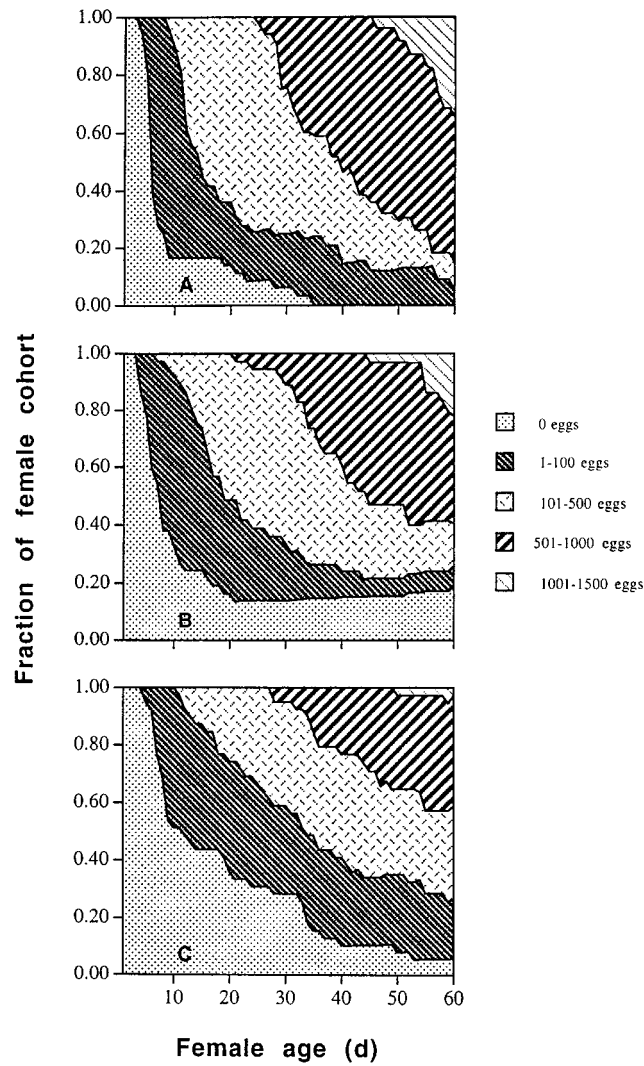
Figure 8. Fraction of females in *P. quatuordecimpunctata* populations that had laid a cumulative total of 0 eggs, 1–100 eggs, 101–500 eggs, 501–1000 eggs, 1001–1500 eggs by age (cumulative parity). A, France; B, Turkey; C, Canada.

daily parity. Therefore, repeatability can also be interpreted as the correlation between the daily parities within each female; the smaller the repeatability the smaller the correlation between daily parities. If the estimate of the daily parity repeatability is closer to 1.0 it means that females lay approximately the same number of eggs every day.

Table 2. Repeatability and variance components of daily parity within geographic populations of *Coccinella septempunctata* and *Propylea quatuordecimpunctata*

Species	Population	Inter-female variance	Intra-female variance	Repeatability
C. septempunctata	Iowa	233.48	502.80	0.32
C. septempunctata	Delaware	306.08	579.24	0.35
C. septempunctata	France	340.24	815.57	0.28
C. septempunctata	Ukraine	336.27	693.80	0.33
P. quatuordecimpunctata	France	32.76	96.50	0.25
P. quatuordecimpunctata	Turkey	39.76	81.41	0.33
P. quatuordecimpunctata	Canada	34.76	63.66	0.35

Discussion

The importance of age at first reproduction in the colonizing ability of organisms was first addressed by Lewontin (1965), who compared the effects of changes in several life history traits on the intrinsic rate of increase, r. He found that, for example, to increase r from 0.510 to 0.565 an organism would need to double its total fecundity from 5000 to 10,000 or decrease its age at first reproduction from 8.6 to 7.5 days. From this and other examples, Lewontin (1965) determined that, in general, 10% reductions in age at first reproduction are approximately equivalent in their effects on r to increases of about 100% in total fecundity. This led him to conclude that species that have 'a long history of colonization' should have low levels of genetic variance in their age at first reproduction and relatively higher levels of variance in fecundity. This is because directional selection will have acted more strongly on the age at first reproduction than on fecundity during the colonizing phase of the invasion process. Roff (1993) pointed out that Lewontin's conclusion applies only to species where r is significantly larger than zero, and that when r is close to zero, a delay in reproduction (i.e. longer preoviposition periods) results in larger r. Therefore, in species with r close to zero, selection should favor delays in reproduction.

Both *Coccinella septempunctata* and *Propylea quatuordecimpunctata* have invaded large parts of North America and are continuing to widen their distributions. Estimates of the intrinsic rate of increase of *C. septempunctata* populations were reported by Phoofolo and Obrycki (1995) to be 0.17 individuals per female per day for the Iowa population, 0.20 for Delaware, 0.19 for France, and 0.18 for Ukraine. The intrinsic rate of increase of *P. quatuordecimpunctata* populations were estimated by Obrycki et al.

(1993) as 0.14 for the Canadian population whereas that of the two Palearctic populations was 0.15. Given that these estimates of r were reported to be statistically different from zero and that the Palearctic populations of both species were collected from their indigenous locations, based on Lewontin's (1965) conclusions, one would have expected them to have more homogeneous preoviposition periods than the Nearctic populations, which have not had 'a long history of colonization'.

Our results, however, show that whereas most females laid their first egg within two weeks of their adult life, the remaining females either had long preoviposition periods or never laid any egg during the 60-day experimental period. Similar results were obtained from *C. septempunctata* populations from the former Czechoslovakia (Hodek, 1966) and France (Bonnemaison, 1966), where it was shown that even after rearing populations for 6 generations, some females still did not lay eggs despite optimal conditions for reproduction (excess prey, long photoperiods, suitable temperature, and relative humidity). Hodek (1966) concluded that this pattern reflected the occurrence of a mixture of univoltine and multivoltine individuals, whereby univoltine individuals are characterized by long preoviposition periods (i.e. diapause) and multivoltine individuals have short preoviposition periods (i.e. no diapause). We previously interpreted this intrapopulation variation in preoviposition periods as evidence of a bet-hedging strategy (Phoofolo and Obrycki, 1995). Bet-hedging strategies in seasonal reproduction have been documented in other aphidophagous predators such as *Chrysoperla carnea* (Tauber and Tauber, 1986, 1992, 1993). Unlike *C. septempunctata*, that is evidently heterogeneous in Europe, *P. quatuordecimpunctata* populations in southeast France are considered to be exclusively multivoltine (Iperti, 1966b). Our results indicate that *P. quatuordecimpunctata* had fewer females with long preoviposition periods compared with *C. septempunctata*. Perhaps this is the reflection of differences in geographical distributions and invasion rates/abilities of these species.

Daily fecundity analyses within each geographic population showed that reproductively mature females have different oviposition rates as shown by the frequency distributions of daily parity classes. Within *C. septempunctata* populations, females had daily fecundities that ranged from zero to >59 eggs per day, whereas within *P. quatuordecimpunctata* populations, daily fecundities ranged from zero to <59. This suggests that the relationship proposed by Stewart et al. (1991) between clutch size and ovariole number in coccinellids (Equation (1)) represents potential rather than realized fecundity. If females laid eggs according to the clutch size-ovariole number relationship, the daily parity classes of 30–59 and >59 eggs would be more represented in *C. septempunctata* whereas the parity class of 1–29 eggs would be less repre-

sented because only females with ovariole numbers of ≤ 58 would contribute to that class. Iperti (1966a) reported the range of ovariole numbers in *C. septempunctata* to be 80–94; this probably represents ovariole numbers of the majority, but not all of the females in this species. The number of ovarioles in *P. quatuordecimpunctata* range from 20–28, which is one-quarter to one-third that of *C. septempunctata* (Iperti, 1966a). The small body size and number of ovarioles of *P. quatuordecimpunctata* females (relative to those of *C. septempunctata*) explain the absence of both the daily parity class of >59 eggs and cumulative parity class of >1500 eggs and the smaller average fecundity.

The within-female component of variation in daily parity was larger than that due to differences among females in all populations of both coccinellid species (Table 2). This provides further evidence that the actual fecundity of a species is not constant (it would be constant if ovariole number was the only determinant of fecundity) but varies on a daily basis. If resources and other environmental conditions are held constant, two other factors besides ovariole number influence actual fecundity in insects: age at mating and mating frequency (Markow, 1982, 1996; Leather, 1988, 1995; Ridley, 1988). During our experiment mating incidences were not continuously monitored; the only mating incidences that we took note of were those that occurred when feeding and egg-counting were done. Therefore, we do not know the extent to which variation in daily fecundity was influenced by mating frequency. But large variation within each female in daily fecundity cannot be explained by the influence of mating frequency in these species, i.e. if mating frequency was a factor, its influence would be observed on the among-individual component of daily fecundity variation. Godfray (1987) and Godfray and Ives (1988) proposed that females do not produce precise clutch sizes but instead they may have evolved reproductive behaviors that promote stochastic oviposition rates as a result of living in temporally and spatially unpredictable environments. Such stochasticity may be evidence of a bet-hedging strategy, an adaptation that results in a variable phenotypic expression of a single genotype, and therefore enabling species to survive in unpredictable, as well as novel, environments (Walker, 1986; Seger and Brockmann, 1987). Estimates of repeatability of daily fecundity were relatively low, indicating that most of the variation in this trait is due to environmental rather than genetic effects; however, during this study, environmental conditions were kept constant as far as we could determine. Low repeatabilities of daily fecundity support the premise that natural selection has utilized most of the genetic variation associated with life-history traits, leading these traits to have relatively lower heritabilities compared with morphological traits not related to fitness (Mousseau and Roff, 1987; Falconer, 1989).

In this paper, we followed the approach of analyzing biological differences among and within individuals. We contend that phenotypic variation, whether or not genetically based, is important for populations to survive in environments that are unpredictable, as well as those that are novel to the species. Therefore, rather than trying to correlate averages of ecological traits to the invasive ability of species (i.e. establishment success of biological control agents), perhaps emphasis should be placed on determining if ability to invade new environments correlates with phenotypic variations of traits that are ecologically important. It is therefore quite possible that the variation in reproductive traits of both *C. septempunctata* and *P. quatuordecimpunctata* have contributed to their establishment and subsequent widespread distribution in North America.

Acknowledgements

References

Bennett, A.F., 1987. Interindividual variability: an underutilized resource. In: M.E. Feder, A.F. Bennett, W.W. Burggren and R.B. Huey (eds), *New Directions in Ecological Physiology*. Cambridge University Press, New York. pp. 147–166.

Bonnemaison, L., 1966. A few observations on the diapause of *Coccinella septempunctata* L. In: I. Hodek (ed), *Ecology of Aphidophagous Insects*. Academia, Praha and Junk, The Hague. pp. 103–104.

Carey, J.R., 1993. *Applied Demography for Biologists with Special Emphasis on Insects*. Oxford University, New York.

Carey, J.R., P. Yang and D. Foote, 1988. Demographic analysis of insect reproductive levels, patterns and heterogeneity: case study of laboratory strains of three Hawaiian tephritids. *Entomol. Exp. Appl.* 46: 85–95.

Crawley, M.J., 1986. The population biology of invaders. *Phil. Trans. Roy. Soc. London* B3114: 711–731.

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 the eastern North America. *Entomol. News* 105: 244–256.

Ehrlich, P.R., 1986. Which animal will invade? In: H.A. Mooney and J.A. Drake (eds), *Ecology of Biological Invasions of North America and Hawaii*. Springer-Verlag, New York. pp. 79–95.

Elliott, N., R. Kieckhefer and W. Kauffman, 1996. Effects of an invading coccinellid on native coccinellids in an agriculture landscape. *Oecologia* 105: 537–544.

Evans, E.W. and A.F.G. Dixon, 1986. Cues for oviposition by ladybird beetles (Coccinellidae): response to aphids. *J. Animal Ecol.* 55: 1027–1034.

Falconer, D.S., 1989. *Introduction to Quantitative Genetics*, 3rd ed. Longman Scientific and Technical, Essex, UK.

Flanders, R.V., D.J. Nelson, R. Deerberg and C.J. Copeland, 1991. *Aphid Biological Control Project: FY90 Project Report*. USDA-APHIS Biological Control Laboratory, Niles, Michigan. 20 pp.

Godfray, H.C.J., 1987. The evolution of clutch size in invertebrates. *Oxford Surv. Evol. Biol.* 4: 117–154.

Godfray, H.C.J. and A.R. Ives, 1988. Stochasticity in invertebrate clutch-size models. *Theor. Popul. Biol.* 33: 79–101.

Hodek, I., 1966. Voltinism and diapuase in aphidophagous insects. In: I. Hodek (ed), *Ecology of Aphidophagous Insects.* Academia, Praha and Junk, The Hague. pp. 97–102.

Hodek, I., 1973. *Biology of Coccinellidae*. Junk, The Hague.

Iperti, G., 1966a. Some components of efficiency in aphidophagous coccinellids of south-east France. In: I. Hodek (ed), *Ecology of aphidophagous Insects.* Academia, Praha and Junk, The Hague. pp. 253.

Iperti, G., 1966b. Voltinism and arrest of development in aphidophagous coccinellids of southeast France. In: I. Hodek (ed), *Ecology of aphidophagous Insects.* Academia, Praha and Junk, The Hague. pp. 105–106.

Lawton, J.H. and K.C. Brown, 1986. The population and community ecology of invading insects. *Phil. Trans. Roy. Soc. London* B314: 607–617.

Leather, S.R., 1988. Size, reproductive potential and fecundity in insects. Things aren't as simple as they seem. *Oikos* 51: 386–390.

Leather, S.R., 1995. Factors affecting fecundity, fertility, oviposition, and larviposition in insects. In: S.R. Leather and J. Hardie (eds), *Insect Reproduction.* CRC Press, Boca Raton. pp. 143–174.

Lessels, C.M. and P.T. Boag, 1987. Unrepeatable repeatabilities: a common mistake. *Auk* 104: 116–121.

Lewontin, R.C., 1965. Selection for colonizing ability. In: H.G. Bakker and G.L. Stebbins (eds), *The Genetics of Colonizing Species.* Academic Press, New York. pp. 77–94.

Lodge, D.M., 1993. Biological invasions: lessons for ecology. *Trends. Ecol. Evol.* 8: 133–137.

MacArthur, R.H. and E.O. Wilson, 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, New Jersey.

Markow, T.A., 1982. Mating systems of cactophilic Drosophila. In: J.S.F. Barker and W.T. Starmer (eds), *Ecological Genetics and Evolution: The Cactus-Yeast-Drosophila Model System.* Academic Press, New York. pp. 273–287.

Markow, T.A., 1996. Evolution of *Drosophila* mating systems. *Evol. Biol.* 29: 73–106.

Mousseau, T.A. and D.A. Roff, 1987. Natural selection and the heritability of fitness components. *Heredity* 59: 181–197.

Obrycki, J.J. and T.J. Kring, 1998. Predacious Coccinellidae in biological control. *Annu. Rev. Entomol.* 43: 295–321.

Obrycki, J.J., D.B. Orr, C.J. Orr, M. Wallendorf and R.V. Flanders, 1993. Comparative developmental and reproductive biology of three populations of *Propylea quatuordecimpunctata* (Coleoptera: Coccinellidae). *Biol. Control* 3: 27–33.

Obrycki, J.J., K.L. Giles and A.M. Ormord, 1998a. Experimental assessment of interactions between larval *Coleomegilla maculata* and *Coccinella septempunctata* (Coleoptera: Coccinellidae) in field cages. *Environ. Entomol*. 27: 1280–1288.

Obrycki, J.J., K.L. Giles and A.M. Ormord, 1998b. Interactions between an introduced and indigenous coccinellid species at different prey denisites. *Oecologia* 117: 279–285.

Obrycki, J.J., N.C. Elliott and K.L. Giles, 1999. Coccinellid introductions: potential for and evaluation of non-target effects. In: P.A. Follett and J.J. Duan (eds), *Nontarget Effects of Biological Control*. Chapter 9. Kluwer Academic Publishers, Boston.

Parsons, P.A., 1983. *The Evolutionary Biology of Colonizing Species*. Cambridge University Press, New York.

Phoofolo, M.W. and J.J. Obrycki, 1995. Comparative life-history studies of Nearctic and Palearctic populations of *Coccinella septempunctata* (Coleoptera: Coccinellidae). *Environ. Entomol*. 24: 581–587.

Phoofolo, M.W., J.J. Obrycki and E.S. Krafsur, 1995. Temperature-dependent ovarian development in *Coccinella septempunctata* (Coleoptera: Coccinellidae). *Ann. Entomol. Soc. Amer*. 88: 72–79.

Ridley, M., 1988. Mating frequency and fecundity in insects. *Biol. Rev*. 63: 509–549.

Roff, D.A. 1993. *The Evolution of Life Histories*. Chapman & Hall, New York.

Roy, J., 1990. In search of the characteristics of plant invaders. In: A.J. di Castri, A.J. Hansen and M. Debussche (eds), *Biological Invasion in Europe and the Mediterranean Basin*. Kluwer Academic Publishers, Dordrecht, The Netherlands. pp. 335–352.

Seger, J. and H.J. Brockmann, 1987. What is bet-hedging? *Oxford Surv. Evol. Biol*. 4: 182–211.

Stewart, L.A., A.F.G. Dixon, Z. Ruzicka and G. Iperti, 1991a. Clutch and egg size in ladybird beetles. *Entomophaga* 36: 329–333.

Stewart, L.A., J.-L. Hemptinne and A.F.G. Dixon, 1991b. Reproductive tactics of ladybird beetles: relationships between egg size, ovariole number and developmental time. *Func. Ecol*. 5: 380–385.

Tauber, C.A. and M.J. Tauber, 1986. Ecophysiological responses in life-history evolution: evidence for their importance in a geographically widespread insect species complex. *Can. J. Zool*. 64: 875–884.

Tauber, C.A. and M.J. Tauber, 1992. Phenotypic plasticity in *Chrysoperla*: genetic variation in the sensory mechanism and in correlated reproductive traits. *Evolution* 46: 1754–1773.

Tauber, M.J. and C.A. Tauber, 1993. Adaptations to temporal variation in habitats: categorizing, predicting, and influencing their evolution in agroecosystems. In: K.C. Kim and B.A. McPheron (eds), *Evolution of Insect Pests: Patterns of Variation*. Wiley, New York. pp. 103–127.

Walker, T.J., 1986. Stochastic polyphenism: coping with uncertainty. *Fl. Entomol*. 69: 46–62.