# Development Times and Age-Specific Life Table Parameters of the Native Lady Beetle Species *Coccinella novemnotata* (Coleoptera: Coccinellidae) and Its Invasive Congener *Coccinella septempunctata* (Coleoptera: Coccinellidae)

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**ABSTRACT** To determine if differences in life history parameters contribute to native species exclusion, immature development times, larval survivorship, reproductive life history parameters, and age-specific life tables were determined for two populations (eastern United States and western United States) of ninespotted lady beetles (*Coccinella novemnotata* Herbst) and one population of sevenspotted lady beetles (*Coccinella septempunctata* L.). Developing larvae were provided an ad libitum diet of pea aphids (*Acyrthosiphon pisum* Harris) at a constant temperature of 25°C. The first and fourth larval stadia of *C. novemnotata* were significantly longer than that of *C. septempunctata*, as was their total development time from egg to newly eclosed adult. Stage-specific developmental mortality was low for both species and did not exceed 7% for the entire development period. The preoviposition period of the two *C. novemnotata* populations was significantly shorter (15–20%) than that of *C. septempunctata*. *C. novemnotata* from both locations laid significantly fewer total eggs than *C. septempunctata* (34–40% fewer) over the 31-d test period, and also fewer eggs per day (37–43% fewer). The net reproductive rate of the *C. novemnotata* populations was 42–50% lower than that of *C. septempunctata* as was *C. novemnotata*'s intrinsic rate of natural increase ($r_m$: 0.1716 and 0.1840 vs. 0.1959 for western and eastern *C. novemnotata* and *C. septempunctata*, respectively).

**KEY WORDS** *Coccinella*, age-specific life table, development, invasive species, intrinsic rate of natural increase

Aphidophagous coccinellids inhabit nearly every terrestrial habitat in North America (Gordon 1985). Most species in the complex are dietary specialists that primarily consume soft-bodied insects in the order Homoptera and the eggs and small larvae of some non-Homopterans (Hodek et al. 2012). They are a well-established means of aphid control in many agroecosystems and save growers considerable amounts of money in aphid control costs (Debach and Rosen 1991).

During the last century, at least 179 nonnative coccinellids were introduced into the United States to help further suppress populations of crop-damaging aphids beyond what our native suite of coccinellids provided (Harmon et al. 2007). About 15% of these introduced species, including *Coccinella septempunctata* L., *Hippodamia variegata* (Goeze), *Harmonia axyridis* Pallas, and *Propylea quatuordecimpunctata* (L.) became established and are now common (Gordon and Vandenberg 1991). Since the introduction of these nonnatives, several native species like *Coccinella transversoguttata richarsoni* Brown, *Adalia bipunctata* (L.), *Cycloneda munda* (Say), *Chilocorus stigma* (Say), *Hippodamia convergens* Guerin-Meneville, and *Coccinella novemnotata* Herbst have experienced marked declines in their geographic distribution and population size (Elliott et al. 1996, Colunga-Garcia and Gage 1998, Harmon et al. 2007, Gardiner et al. 2011). Several hypotheses that seek to explain the decline of native lady beetles have been put forth, ranging from the loss of habitat through the succession of large amounts of farmland that historically supported large populations of natives (Harmon et al. 2007) to interspecific competition and intraguild predation (Gardiner et al. 2011, Losey et al. 2012, Smith and Gardiner 2013).

One species in particular, *C. novemnotata*, which had been commonplace in agroecosystems throughout North America before the introduction and establishment of *C. septempunctata* (reported in 1973), has been impacted severely. Wheeler and Hoebeke (1995) compiled evidence of *C. novemnotata*'s relative abundance before and after *C. septempunctata*'s establishment and showed that the decline of *C. novemnotata* correlated strongly with the rise of *C. septempunctata*, although they are careful to acknowledge that they cannot derive a causal relationship from their

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data. Numerous other researchers (Hoogendoorn and Heimple 2004, Snyder et al. 2004, Cottrell 2007, Gardiner and Landis 2007) have since gone on to conduct research that sought to explain the decline of native lady beetles, including *C. novemnotata*, and delineate probable mechanisms underlying the declines. Losey et al. (2012) posits several mechanisms of negative interactions between introduced and native coccinellids. The list includes intraguild predation, scramble competition for prey, competition for nonprey resources, the introduction of parasitoids or pathogens, and hybridization.

One avenue of research that has yet to be fully explored and which will drive the intensity of negative interactions is potential differences in the development and demographical parameters of *C. novemnotata* and *C. septempunctata* and how that relates to population growth. While several research groups have published data on development times and reproduction of *C. septempunctata* or *C. novemnotata* (McMullen 1967; Phoofolo and Obrycki 1995, 2000; ElHag and Zaitoon 1996; Xia et al. 1999) many were based on just a few insects and all of the studies use different rearing methods and environmental conditions, including different aphid species as food and incubation temperatures. This makes it difficult to generate useful comparison between the two lady beetle species. While ElHag and Zaitoon (1996) report on the biological parameters of *C. novemnotata* and *C. septempunctata*, their research was based on populations derived from Buraydah, Saudi Arabia, and had very small sample sizes ($n = 8$). We wanted to conduct more robust studies using the same two species, but from collections made within the United States, to gain a better understanding of the factors that may have led to *C. novemnotata*'s decline. Toward that end, we performed a series of experiments that compared the development times and stage-specific rates of mortality of the different life stages of these two coccinellid species, and we also quantified their reproductive output. Using this data, we constructed and compared the age-specific life table parameters of these species.

## Materials and Methods

**Insect Colony Maintenance.** Fava bean seeds (*Vicia faba* L., Gourmet Store, Waukegan, IL), four per 10.2-cm-diameter pot, were placed 4–5 cm deep into Lambert (Quebec City, QC, Canada) LM-series professional growing media. The pots were maintained in a greenhouse at $25 \pm 3°C$ with overhead high-pressure sodium lights set to a photoperiod of 16:8 (L:D) h, and were watered daily. After 8 d of growth, pots were relocated to a walk-in environmental chamber set to a constant $25 \pm 2°C$ and a photoperiod of 16:8 (L:D) h with an overhead fluorescent light. Forty to sixty mixed-age pea aphids, *Acyrthosiphon pisum* Harris, were added to the soil of pots and allowed to distribute themselves among the plants. Aphids were harvested from these bean plants after 7–10d for use as beetle food.

Adult *C. septempunctata* and *C. novemnotata* collected from Oregon, South Dakota, and New York during 2012 were used to generate laboratory colonies (c.a. 20–40 individuals for each group). Adult *C. novemnotata* that were collected from Oregon and South Dakota were pooled and were designated "western *C. novemnotata*." Because *C. novemnotata* collected from Long Island, NY, have a slightly different elytral spotting pattern and likely represent a genetically distinct population, they were maintained as a separate colony and were designated "eastern *C. novemnotata*." Lady beetles were maintained individually in clear 44-ml clear-lidded plastic portion cups that contained a 2.5 by 7 cm piece of paper towel. Paper towels and plastic cups were replaced every 2–3 d. The lady beetles in the colonies were provided freshly collected pea aphids daily (ad libitum) and were maintained at constant $25 \pm 1°C$ and a photoperiod of 16:8 (L:D) h.

**Development Rates of Immature Lady Beetle.** Clutches of lady beetle eggs from each colony were collected every 24 h from cups containing a single mated female. The date of oviposition was recorded. Eggs were monitored daily for larval emergence, which was also recorded to estimate the duration of the egg stage. On the day of egg hatch, larvae were placed singly into 44 ml portion cups and aphids were added ad libitum. Insect state (larval instar, pupa, adult, and alive or dead) was monitored every 24 h and recorded until adulthood, at which time the sex of each individual was determined and recorded. The experiment was conducted twice with the tests being separated by an interval of 1 wk, using eggs laid by different generations of females. For each repetition of the test, 24 insects per lady beetle colony were monitored. The insects were maintained in an environmental cabinet at $25 \pm 1°C$ and a photoperiod of 16:8 (L:D) h. Temperature was recorded every 15 min using a Hobo electronic data logger (Onset Computer, Bourne, MA).

**Reproduction.** Adult lady beetles were produced using the same protocol as described in the development portion of this study, except that an excised fava bean leaf was added to each cup and it was exchanged daily during larval development and up to the day that insects were placed together for mating. Male *C. septempunctata* and *C. novemnotata* do not typically mate until at least 4 d posteclosion and sometimes as much as 8 d posteclosion (T.A.U., unpublished data). To estimate the preoviposition period of adult females, which will mate and lay eggs before being 8-d-old adults, two cohorts of adults were produced about 1 wk apart. Two-, three-, and four-day-old adult female lady beetles were paired with an arbitrarily selected 8-d-old male in 44-ml portion cups (one pair per cup). Pairs were observed for mating, and when copulations ended the male was removed from the cup and a single piece of paper towel (2.5 by 7 cm) was added to the cup, as were aphids (ad libitum) and a single excised fava bean leaf. Cups were sealed with a plastic lid and incubated at constant $25 \pm 1°C$ and a photoperiod of 16:8 (L:D) h. Every 7 d, all surviving females were

**Table 1.   Mean developmental times (±SE) of *C. septempunctata* and *C. novemnotata* life stages maintained at constant 25°C and provided *A. pisum* ad libitum**

| Species | Development time (d) | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Egg | First instar | Second instar | Third instar | Fourth instar | First–fourth | Pupa | Egg to adult |
| *C. septempunctata* | $3.0 \pm 0.0^a$ | $2.1 \pm 0.0a\ (47)^b$ | $1.6 \pm 0.1a\ (46)$ | $2.0 \pm 0.5a\ (46)$ | $4.5 \pm 0.1a\ (46)$ | $10.2 \pm 0.1a\ (46)$ | $5.1 \pm 0.1a\ (46)$ | $18.3 \pm 0.1a\ (46)$ |
| *C. novemnotata* (eastern) | $3.0 \pm 0.0$ | $2.8 \pm 0.1\ b\ (44)$ | $1.8 \pm 0.1a\ (44)$ | $2.3 \pm 0.1a\ (43)$ | $5.1 \pm 0.1b\ (42)$ | $12.0 \pm 0.2b\ (42)$ | $5.3 \pm 0.1a\ (41)$ | $20.2 \pm 0.3b\ (41)$ |
| *C. novemnotata* (western) | $3.0 \pm 0.0$ | $2.9 \pm 0.1\ b\ (48)$ | $1.6 \pm 0.1a\ (48)$ | $2.2 \pm 0.1a\ (48)$ | $5.1 \pm 0.1b\ (46)$ | $11.9 \pm 0.1b\ (46)$ | $5.4 \pm 0.1a\ (45)$ | $20.3 \pm 0.1b\ (45)$ |
| | | $F_{(2,\ 135.1)} = 49.6$ | $F_{(2,\ 134.0)} = 0.16$ | $F_{(2,133.3)} = 2.8$ | $F_{(2,\ 130)} = 14.5$ | $F_{(2,\ 128)} = 55.7$ | $F_{(2,\ 135.1)} = 49.6$ | $F_{(2,\ 127)} = 64.5$ |
| | | $P < 0.0001^d$ | $P = 0.85$ | $P = 0.06$ | $P < 0.0001$ | $P < 0.0001$ | $P < 0.0001$ | $P < 0.0001$ |

[a] Development times (d) of *C. septempunctata* and *C. novemnotata* maintained at constant 25°C and monitored at 24-h intervals.

[b] Numbers in parentheses represent the number of insect completing the respective life stage.

[c] Means ± SE within columns followed by same letter are not significantly different (Tukey–Kramer test, alpha = 0.05).

[d] F-ratio and P value from parametric ANOVA of log-transformed data (within-column test).

provided with males of breeding age and were mated again. The total number of eggs laid each day, including those that were partially cannibalized, was recorded for 31 d with the aid of a dissecting microscope. We also recorded the day of death of the female lady beetles. These data were used to determine the preoviposition period and the number of eggs laid per day for *C. septempunctata* and the two *C. novemnotata* populations. In total, 28, 35, and 31 female *C. septempunctata* and eastern and western *C. novemnotata*, respectively, were followed across two independent test periods.

**Statistical Analysis.** All statistical analyses were conducted using SAS software (SAS Institute 2011, Cary, NC) or JMP Pro 9 (SAS Institute). Developmental times were expressed in units of days and developmental changes were assumed to occur at the midpoint of a 24-h interval. Mixed-model analyses of variance (ANOVA) investigating the effect of "group" on immature life stage duration (larva and pupa) were conducted using data from all insects that completed that life stage. The group effect combined lady beetle species and point of origin for *C. novemnotata.* The three groups were eastern and western *C. novemnotata* and *C. septempunctata.* Experimental repetition (date) was included as a random blocking factor. Sex was not determined for insects that died prematurely, and thus ANOVAs that included sex as a main effect included only those insects that completed development to adulthood. Time-to-event response data like time for completion of a life stage or time to death are generally not normally distributed. Therefore, each analysis was confirmed by an additional ANOVA after rank transformation of the data, a procedure equivalent to the nonparametric Kruskal–Wallis test (Conover 1999). Results regarding significance of main effects from ANOVA of the rank-transformed data were compared with those from parametric ANOVA and if the results from the two analyses were not different, the findings of the parametric ANOVA were accepted and presented. Post hoc analyses were conducted using Tukey's honestly significant difference (HSD) at an overall alpha = 0.05.

The preoviposition period, total number of eggs laid, and the number of eggs laid per egg-laying day (total eggs per 31-d test period − preoviposition period) were analyzed using mixed-model ANOVA that included a random block (date) factor and a fixed "group" effect, as described above. Data were untrans-

formed for analyses. Lady beetle survival to the adult stage was analyzed via nominal logistic regression using PROC GENMOD. Post hoc analyses, where appropriate, were conducted using Tukey's HSD test at alpha = 0.05.

Survivorship data for each life stage, expressed as days alive, was used to calculate age-specific life tables. Daily survivorship and age-specific fecundity of adult females were used to estimate the intrinsic rate of natural increase ($r_m$) for each lady beetle group using the following formula: $\Sigma\ (e^{-rx}) l_x m_x = 1$, where $x$ = age of the adult lady beetle, $l_x$ = proportion surviving on day $x$, and $m_x$ = female eggs per female on day $x.$ The number of female eggs per female laid on day $x$ was calculated by dividing the total eggs per day by two. The sex ratio of the adults that emerged in the development study (see Results) suggested a 1:1 sex ratio. The net reproductive rate ($R_0$) was calculated using the equation $R_0 = \Sigma\ l_x m_x$; generation time ($T$) and doubling time ($DT$) for each temperature were calculated using equations $T = \ln R_0 / r_m$ and $DT = \ln 2 / r_m$, respectively, as per Birch (1948). Population growth for each lady beetle group was estimated over a 100-d period using the equation $N_t = N_0 e^{rt}$ where $N_0$ is the initial number of lady beetles, $r$ is the intrinsic rate of natural increase under optimal conditions, $t$ is the elapsed time, and $e$ equals the constant 2.7182.

## Results

**Development Rates of Immature *C. novemnotata* and *C. septempunctata.*** There was a significant effect of beetle group on the total development time from the egg stage to newly eclosed adult ($F_{(2,\ 127)} = 64.5$; $P < 0.0001$; Table 1). Each *C. novemnotata* population developed significantly slower (9–10%) than *C. septempunctata*, but did not differ from each other ($F_{(1,\ 82)} = 0.34$; $P = 0.56$). The difference in the overall development time of *C. septempunctata* can be attributed to its significantly faster development during first and fourth instars (Table 1; Fig. 1). During these two stadia *C. septempunctata* developed 0.7 d (25%) and 0.6 d (12%) faster, respectively, than both *C. novemnotata* populations (Table 1). There was not a significant main effect of beetle sex on the total development time from egg to adult ($F_{(1,\ 127)} = 0.11$, $P = 0.74$). The total development time of male eastern and western *C. novemnotata* and *C. septempunctata* was 20.2 ±
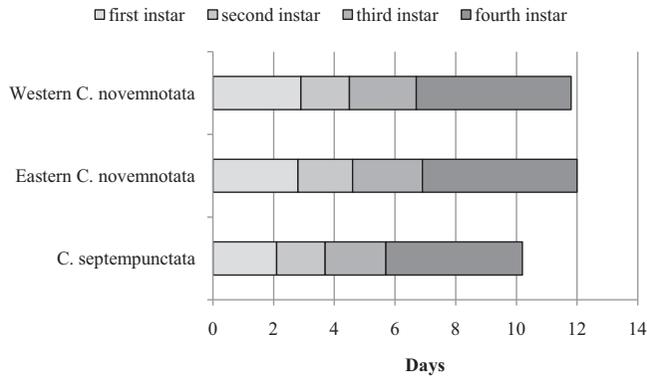
**Fig. 1.** Depiction of length of the larval stadia illustrating the degree of overlap among the instars of three lady beetle groups.

0.3, 20.4 ± 0.2, and 18.4 ± 0.1 d, respectively, and for females, total development times were 20.3 ± 0.4, 20.1 ± 0.1, and 18.3 ± 0.1 d, respectively. There was no effect of the beetle sex × group interaction ($F_{(2,\,125)}$ = 1.6; $P$ = 0.20).

The survival of all three groups of lady beetles to adulthood was high (>93%; Table 2) and did not differ significantly from each other ($\chi^2$ = 0.36; df = 2; $P$ = 0.84). Developmental stage-specific mortality ($d_x$, percentage mortality with respect to the total number of individuals entering a stadium) was low and never reached >5% during any stadium for either *C. novemnotata* population or *C. septempunctata.* Across lady beetle groups, fourth-instar larvae suffered the greatest rates of mortality at 2.1%.

**Reproduction.** The preoviposition period (number of days between eclosion and first egg laying) among the different lady beetle groups was significantly different ($F_{(2,53.7}$ = 4.2; $P$ = 0.02). *C. septempunctata* had a slightly longer preoviposition period (5.5 ± 0.3 d; Table 2) than western *C. novemnotata* (4.4 ± 0.2 d), but not from eastern *C. novemnotata* (4.7 ± 0.3 d), and the two *C. novemnotata* populations did not differ from

one another. Over the 31 d posteclosion, *C. septempunctata* laid significantly more eggs than the eastern and western *C. novemnotata* populations (1.5 and 1.7 times more, respectively; $F_{(2,86.3)}$ = 9.8; $P$ = 0.0001), and the two *C. novemnotata* populations did not differ from each other (Table 3). Similarly, *C. septempunctata* laid significantly more eggs per day than either *C. novemnotata* population ($F_{(2,87.5)}$ = 12.9; $P < 0.0001$). Daily offspring production per surviving female, referred to as the age-specific rate of offspring production, was plotted for each lady beetle group and is presented in Fig. 2. It is important to note that age-specific means and their SEs are based on decreasing numbers of females over time; as females die they are removed from the calculations. The survival of adults to the end of the 31-d test period differed significantly as a function of lady beetle group ($\chi^2$ = 15.0; df = 2; $P$ = 0.0006) and can also be seen in Fig. 2. Eastern *C. novemnotata* survival to 31 d was significantly lower (46% survival) than both western *C. novemnotata* and *C. septempunctata* (65 and 89% survival, respectively), which did not differ from each other. Cohort-specific daily egg production (mean ± SE number of eggs laid

**Table 2.** Species and geographic-stain-dependent mortality of immature *C. septempunctata* and *C. novemnotata* reared at constant 25°C on *A. pisum* that were provided ad libitum

| | Life stage | $a_x$ (no. alive at start of life stage) | $l_x$ (percentage of original cohort surviving to the next stage) | No. dying during each stadium | $d_x$ (percentage of original cohort dying during each stage) | $q_x$ (stage specific percentage mortality) |
|---|---|---|---|---|---|---|
| Eastern *C. novemnotata* | First | 44 | 100 | 0 | 0.0 | 0.0 |
| | Second | 44 | 100 | 0 | 0.0 | 0.0 |
| | Third | 44 | 100 | 1 | 2.3 | 2.3 |
| | Fourth | 43 | 97.7 | 1 | 0.0 | 2.3 |
| | Pupa | 43 | 97.7 | 1 | 4.5 | 2.3 |
| | Adult | 41 | 93.2 | | | |
| Western *C. novemnotata* | First | 48 | 100 | 0 | 0.0 | 0.0 |
| | Second | 48 | 100 | 0 | 0.0 | 0.0 |
| | Third | 48 | 100 | 0 | 0.0 | 0.0 |
| | Fourth | 48 | 100 | 2 | 4.2 | 4.2 |
| | Pupa | 46 | 95.8 | 1 | 2.1 | 2.2 |
| | Adult | 45 | 93.8 | | | |
| *C. septempunctata* | First | 48 | 100 | 1 | 2.1 | 2.1 |
| | Second | 47 | 97.9 | 1 | 2.1 | 2.1 |
| | Third | 46 | 95.8 | 0 | 0.0 | 0.0 |
| | Fourth | 46 | 95.8 | 0 | 0.0 | 0.0 |
| | Pupa | 46 | 95.8 | 0 | 0.0 | 0.0 |
| | Adult | 46 | 95.8 | 0 | | |

**Table 3.** Mean (±SE) preoviposition period, egg-laying days, and daily and total fecundity for eastern and western *C. novemnotata* and *C. septempunctata* maintained for 30 d posteclosion at constant 25°C on an ad libitum diet of *A. pisum*

| Species | $n^a$ | Preoviposition period[b] | Total eggs[b] | Eggs per day[b] | Percentage survival to 31 d posteclosion |
|---|---|---|---|---|---|
| *C. septempunctata* | 28 | 5.5 ± 0.3a | 1050.3 ± 72.1a | 41.1 ± 2.7a | 89.3%a |
| *C. novemnotata* (eastern) | 35 | 4.7 ± 0.3ab | 690.5 ± 66.6b | 26.0 ± 2.5b | 45.7%b |
| *C. novemnotata* (western) | 31 | 4.4 ± 0.2b | 623.3 ± 66.2b | 23.3 ± 2.4b | 64.5%a |

[a] Total number of female lady beetles followed for reproduction studies.
[b] Means (±SEs) within a column followed by the same letter are not significantly different (Tukey–Kramer HSD; alpha = 0.05).

per females entering the test) by the three lady beetle groups are plotted in Fig. 3 and show the rate of daily egg laying at the population level.

**Demographical Growth Parameters.** The demographical growth parameters of the three lady beetle groups are presented in Table 4. The intrinsic rate of
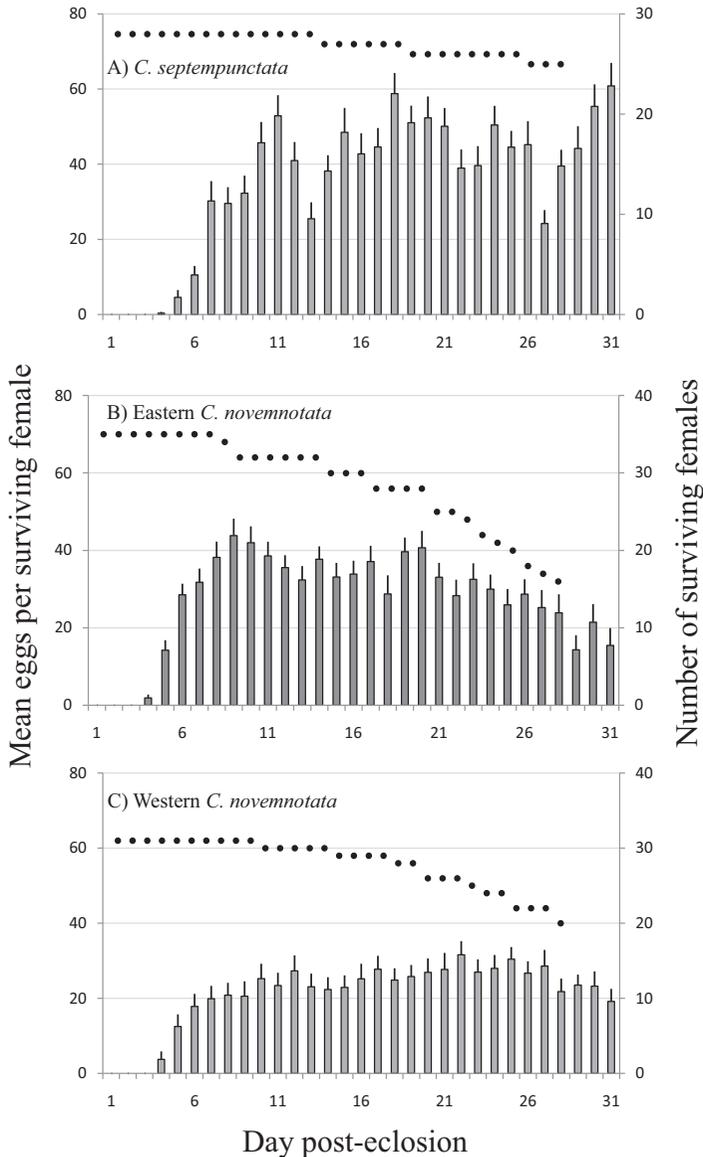


**Fig. 2.** Age-specific mean (±SE) daily rate of egg production (bars) and survival (dots) of adult female *C. septempunctata* (A), eastern *C. novemnotata* (B), and western *C. novemnotata* (C) reared at constant 25 ± 1°C. Means are based on a decreasing number of females over time.
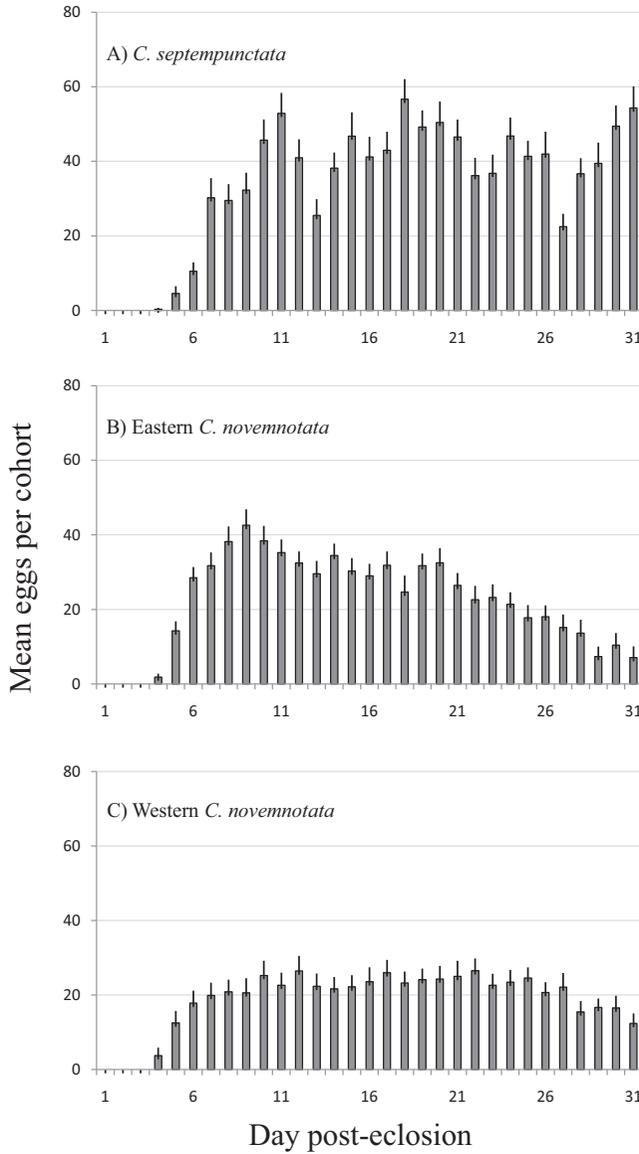
**Fig. 3.** Cohort-specific mean (±SE) daily rate of egg production (bars) and survival (dots) of adult female *C. septempunctata* (A), eastern *C. novemnotata* (B), and western *C. novemnotata* (C) reared at constant 25 ± 1°C. Means and SEs are based on all females tested without removal of dead individuals from the calculations.

**Table 4.   Intrinsic rate of increase ($r_m$), net reproductive rate ($R_0$), generation time (*GT*), and doubling time (*DT*) for eastern and western *C. novemnotata* and *C. septempunctata* maintained for 31 d posteclosion at constant 25 ± 1°C on an ad libitum diet of *A. pisum***

| Species | $n^a$ | $R_m$ | $R_0$ | GT (d) | DT (d) | Population size after 100 d of growth |
|---|---|---|---|---|---|---|
| *C. septempunctata* | 28 | 0.1959 | 549.0 | 32.2 | 3.5 | $3.2 \times 10^8$ |
| *C. novemnotata* (eastern) | 35 | 0.1840 | 321.1 | 31.4 | 3.8 | $9.8 \times 10^7$ |
| *C. novemnotata* (western) | 31 | 0.1716 | 273.5 | 32.7 | 4.0 | $2.8 \times 10^7$ |

[a] Total number of female lady beetles from which life table parameters were estimated.

natural increase, $r_m$, was larger (0.1959) for *C. septempunctata* than for eastern and western *C. novemnotata* (0.1840 and 0.1716, respectively). When the population growth of the three lady beetle groups was simulated >100 d (a single iteration of the population growth equation with $t = 100$) with the initial population sizes of all groups equal to 1, the *C. septempunctata* population was 3.3 and 11.4 times larger than eastern and *C. novemnotata* populations, respectively. The net reproductive rate of *C. septempunctata* was 1.7 and 2.0 times greater than eastern and western *C. novemnotata* populations, respectively, and the generation times were very similar for all lady beetle groups.

## Discussion

The development time of *C. novemnotata* from the egg stage to newly eclosed adult was significantly slower than that of its invasive congener *C. septempunctata* when both were reared at 25°C on an ad labium diet of *A. pisum.* This difference was largely an effect of the slower development of first- and forth-instar larvae, which resulted in a 2 d (10%) difference in development times among the species. ElHag and Zaitoon (1996) reared *C. novemnotata* and *C. septempunctata* on a mixed diet of *Brevicoryne brassicae* (L.) and *Rhopalosiphum padi* L. at 25°C and reported that there was not a significant difference in the total development times of the two species (21.0 vs. 20.0 d, respectively), and their total development times were similar to that of the two *C. novemnotata* populations used in this study. The total development times of our *C. novemnotata* populations were also similar to that reported by McMullen (1967), which we estimated via interpolation of development times that were presented over a range of temperatures. The total development time of *C. septempunctata* in this study was similar to that reported in Hauge et al. (1998), Xia et al. (1999), Kalushkov and Hodek (2004), but different from what has been reported by Phoofolo and Obrycki (1995) and Kontodimas et al. (2008). Xia et al. (1999) reports that the adult emergence data of *C. septempunctata* reared at 25°C was 28 d, and Phoofolo and Obrycki (1995) report development times 13–20% faster that what we report. The reason for these differences is unclear, but may be partially a function of the slightly higher rearing temperature used in some of the experiments (26 ± 1°C), or it may be a result of normal genetic variation among the various populations used.

The significantly faster development time of *C. septempunctata* compared with *C. novemnotata* has important practical implications. Turnipseed et al. (2014) showed that when same-aged first-instar larvae of these two species were reared to adulthood together in the same cup, that *C. novemnotata* suffered significant rates of intraguild predation; only 15–55% survival depending on the density of aphids that was provided to the pair. Turnipseed et al. (2014) conducted a second study that paired first-, second-, or third-instar *C. novemnotata* with either a first- or second-instar *C. septempunctata,* and showed that *C. novemnotata* survival increased as the age differential and size differential between the two species increased. The difference between the development times of these two species implies that, on average, *C. septempunctata* will be more developmentally advanced than *C. novemnotata.* If these results can be extended to field populations, this may be one factor that contributed to the decline of *C. novemnotata,* and warrants further investigation.

Cumulative developmental mortality was low for all of the lady beetle groups used in this study (<7%). Our rates of mortality were similar to those presented for *C. novemnotata* (McMullen 1967) and *C. septempunctata* (Phoofolo and Obrycki 1995, Kalushkov and Hodek 2004, Kontodimas et al. 2008, Ali and Rizvi 2010). However, ElHag and Zaitoon (1996), Hauge et al. (1998), and Xia et al. (1999) reported rates of developmental mortality ranging from ≈45–75%. It is interesting to note that in two of the three studies that reported high rates of survival to the adult stage, 1ids were supplied as the food source, whereas those studies that had high levels of developmental mortality were never provided pea aphids for food. Kalushkov and Hodek (2004) report the survival of *C. septempunctata* reared on 13 different aphid species and they never observed >10% mortality during development from the egg to the adult stage. The reasons for the large disparity in the rates of developmental mortality among these studies are not clear, but given the high rates of survivorship of *C. septempunctata* when reared on such a wide variety of aphids species (Kalushkov and Hodek 2004), one might reasonably suspect handling mortality or pathogens such as microsporidia are partially responsible.

The durations of the preoviposition period of the two *C. novemnotata* populations used in this study were slightly shorter than that of *C. septempunctata,* although they were all within ≈1 d of each other. They corresponded closely to those reported for *C. novemnotata* in McMullen (1967), and *C. septempunctata* in Phoofolo and Obrycki (1995), but were much shorter (2.0–3.75 times shorter) than what was reported for *C. septempunctata* in Xia et al. (1999) and Phoofolo and Obrycki (2000).

Both of our *C. novemnotata* populations laid significantly fewer eggs (34–40% fewer) during the 31 d postadult eclosion than *C. septempunctata.* This can be partially explained by the greater rates of adult *C. novemnotata* mortality compared with *C. septempunctata* over the 31-d observation period. However, comparison of the daily rate of egg production removes the bias associated with comparisons of fecundities based on different numbers of egg-laying days, and both *C. novemnotata* populations also laid significantly fewer eggs per day than *C. septempunctata.* The *C. novemnotata* populations in this study laid many more eggs in 31 d compared with what McMullen (1967) and ElHag and Zaitoon (1996) report for the lifetime fecundity of *C. novemnotata,* and the daily rates of egg production of both *C. novemnotata* and *C. septempunctata* were at least twice as high as reported in Phoofolo and Obrycki (1995, 2000), ElHag and Zaitoon (1996), Xia et al. (1999), Kalushkov and Hodek (2004), and Kontodimas et al. (2008). *C. septempunctata* has also been implicated in the decline of *C. transversoguttata,* another native North American ladybeetle. Kajita and Evans (2010a,b) and Kajita et al. (2009) showed in a series of studies that *C. septempunctata* laid more eggs than *C. transversoguttata* and that *C. septempunctata* begins laying eggs earlier in the season. The greater reproductive capacity of *C. septempunctata* compared with native species in decline appears to be a common theme that warrants further investigation at a range of prey densities and environmental conditions.

One important and useful application of life history data are that it allows for the calculation of the intrinsic rate of natural increase, which takes into account all of the relevant life history parameters of a species: the development time and rates of survival of the immature stages of a species, and the preoviposition period, sex ratio, daily rate of egg production, and rates of mortality of adults females. This has the effect of standardizing the relevant life history parameters of species and can make for very useful, normalized comparisons among species. The one parameter in the calculation that is left to the experimenter that can impact its result is the number of days that fecundity data are recorded over, which is not problematic if the period is sufficiently long. For *C. novemnotata* and *C. septempunctata* in this study, the intrinsic rate of natural increase is heavily weighted by reproduction during the first 18–20 d, which consequently is equal to the total development time from the egg stage to a newly eclosed adult. *C. septempunctata* in this study had a slightly higher intrinsic rate of natural increase than both *C. novemnotata* populations, and were similar to those reported for *C. septempunctata* by Phoofool and Obrycki (1995), but much higher than those reported in ElHag and Zaitoon (1996) and Kontodimas et al. (2008). The intrinsic rate of natural increase is also commonly referred to as the instantaneous rate of population growth. Its scale in this study is at the per day level, and small differences between species are quickly compounded over time, which is more easily observed by applying the equation for modeling population growth over a specified length of time.

The results of the experiments presented herein showed that *C. septempunctata* developed significantly faster than *C. novemnotata* and laid significantly more eggs at a faster rate than *C. novemnotata* at 25°C when provided with unlimited prey. This resulted in an overall greater rate of population growth of this invasive species. When this information is coupled with the fact that *C. septempunctata* is significantly more voracious than *C. novemnotata* (Hoki et al. 2014), and that it exerts significant levels of intraguild predation against *C. novemnotata* (Turnipseed et al. 2014), it becomes more difficult to reject the hypothesis that *C. septempunctata* contributed to the decline of *C. novemnotata* and potentially other native lady beetle species. Additional laboratory and field-based studies that examine the interactions of *C. septempunctata* and native lady beetle species would greatly enhance our understanding of what forces led to the decline of native species and what is preventing them from reversing their declines. Specifically, studies that investigate the effect of prey density and temperature on parameters such as development time, foraging ability, leaving time from a patch of aphids, reproductive output, and intraguild predation would be useful. They would also serve to confirm or refute *C. septempunctata*'s status as the causal agent of native lady beetle decline.

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