Temperature-Dependent Development, Survival, Longevity, and Fecundity of *Propylea quatuordecimpunctata* (Coleoptera: Coccinellidae)

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Ann. Entomol. Soc. Am. 106(2): 228Ð234 (2013); DOI: http://dx.doi.org/10.1603/AN12104

ABSTRACT The effect of temperature on the development, survival, longevity, and fecundity of the 14-spotted ladybird beetle, *Propylea quatuordecimpunctata* L. (Coleoptera: Coccinellidae) reared on bean aphid, *Aphis fabae* Scopoli (Hemiptera: Aphididae) was determined at six constant temperatures (17, 20, 25, 30, 32.5, and 35°C) in the laboratory. Results showed a temperature-dependent development of the coccinellid. An appropriate linear model indicated that 218.0 degree days above a threshold of 10.2°C were needed to complete immature development from egg to adult emergence. Data were fitted to the nonlinear Briere model, which for total immature period estimated the upper developmental threshold at 36.0°C, the lower threshold at 12.2°C and the temperature for maximum developmental rate at 30.3°C. Survival of immature stages varied significantly across temperatures with the lowest survival of just 14% occurring at 32.5°C and the highest (96%) at 25°C. In addition temperature showed a profound effect on female longevity over this viable range of temperatures, as it decreased from 123.06 d at 17°C to 33.53 d at 30°C. The highest fecundity (724.6 eggs/female) was recorded at 25°C. These results might be useful tools for the prediction of *P. quatuordecimpunctata* phenology and the interaction with its prey.

KEY WORDS *Aphis fabae*, development, fecundity, *Propylea quatuordecimpunctata*, temperature

In terms of biological control, knowledge of thermal thresholds and thermal summation (the amount of energy needed to complete a developmental process often measured as degree-days), as well as the thermal window, that is, the range of temperatures over which a predator can grow and reproduce (Dixon et al. 2009), could be useful for the prediction of its phenology and coexistence with its prey. Temperature sets limits for trophic interactions among species of poikilotherms and may influence the level of control by natural enemies (Huffaker et al. 1971).

Aphids are recognized as serious pests in crops and wild plants worldwide, directly and indirectly affecting infestations. The development of an integrated pest management (IPM) program to control aphid populations often includes some reliance on natural enemies such as parasitoids and predators. Predaceous coccinellids are well-known predators of aphids and coccids (Dixon 2000). Although coccidophagous ladybird beetles have been more successful biological control agents than aphidophagous species, mainly because of their ability to develop faster than their prey (Dixon 2000), aphidophagous species cause significant mortality to aphid pests in a number of agricultural systems (Obrycki et al. 2009).

A common aphidophagous predator that is widely distributed in the Palearctic region, and that has also been introduced to and established in the Nearctic region (Day et al. 1994), is the 14-spotted ladybird beetle, *Propylea quatuordecimpunctata* L. (Coleoptera: Coccinellidae). Although Hämläinen et al. (1975) and Kalushkov and Hodek (2005) claimed that this species is probably a poor aphid predator based on its relatively small effect against the green peach aphid, *Myzus persicae* (Sulzer), populations, Papanikolaou et al. (2011) reported an inverse density dependent mortality of its aphid prey. We studied the influence of temperature on the development, survival, longevity, and fecundity of this predator and sought to estimate the thermal thresholds and thermal summation for immature stages of *P. quatuordecimpunctata* using its prey, the bean aphid, *Aphis fabae* Scopoli (Hemiptera: Aphididae) as its source of food.

Materials and Methods

Insects. The coccinellids were collected in summer 2006 from corn, *Zea mays* L., plants infested by the corn leaf aphid, *Rhopalosiphum maidis* Fitch, in Arta
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County (Northwestern Greece, 21° 00′/39° 10′0′). P. quatuordecimpunctata beetles were reared on A. fabae infesting potted fava bean, Vicia faba L., plants in cylindrical Plexiglas cages (50 × 30 cm) at 25 ± 1°C, 65 ± 5% relative humidity (RH), and a photoperiod of 16:8 (L:D) h. An A. fabae colony (originally from a stock colony at the Biological Control Laboratory, Benaki Phytopathological Institute) was reared on V. faba plants at 20 ± 1°C (65 ± 2% RH, 16:8 [L:D] h). Before conducting the experiment, a P. quatuordecim-

Experimental Set-Up. P. quatuordecimpunctata egg masses (<12-h-old) were transferred from the stock culture into cylindrical Plexiglas cages (5 × 10 cm) containing A. fabae nymphs and adults. The cages with beetle eggs were then randomly assigned to treatments and placed in six environmental chambers (SANYO, model MLR-3500TF, 3500HT). We used six treatment temperature regimes (17, 20, 25, 30, 32.5, and 35 ± 1°C). Irrespective of the temperature, all environmental chambers were set to 65 ± 2% RH and a photoperiod of 16:8 (L:D) h. Initial egg densities were 35, 30, 26, 40, and 100 at 17, 20, 25, 30, and 32.5°C, respectively, allocated to three cages except for the 32.5°C where they allocated to five cages. After hatching, larvae were kept individually with aphids offered ad libitum. The duration and survival of egg, larval, and pupal stages were recorded every 12 h.

Adults emerged from pupae at each temperature regime were used for determining female longevity and fecundity. When numbers of male–female pairs were not sufficient for statistical analysis, we used additional pairs of adults that had completed the immature development at the same conditions as those of the developmental study. Female longevity and fecundity were examined at 17, 20, 25, and 30°C and at 65 ± 2% RH and a photoperiod of 16:8 (L:D) h. Formed pairs were kept separately in cylindrical Plexiglas cages (5 × 10 cm). We used 16, 20, 25, and 15 pairs at 17, 20, 25, and 30°C, respectively. Each day aphids were added in the cages ad libitum and beetle eggs were counted and removed. Observations continued until the females died.

Statistical Analyses. Data on immature development and female longevity were subjected to the Shapiro–Wilk normality test, which indicated departure from a normal distribution. Therefore, data were analyzed by Kruskal–Wallis analysis of variance (ANOVA) on ranks (α = 0.05). Kruskal–Wallis test was also used for the analysis of fecundity data. χ² test was performed to compare survival of egg, larva, pupa, and total immature periods at different constant temperatures.

The relationship between temperature and development rate was described by the nonlinear Briere model (Briere et al. 1999). The Briere model is perceived to possess a reasonable balance between mathematical tractability and biological realism. Therefore, it is suitable for estimating minimum threshold temperature for development (Kontodimas et al. 2004, Dixon et al. 2009). The relationship between temperature and development was also described by the linear regression model of Ikemoto and Takai (2000).

The mathematical expressions of Briere (1) and Ikemoto and Takai (2) models are:

\[ r(T) = \alpha \times T \times (T - T_0) \times \sqrt{T_L - T} \]

\[ (D \times T) = K + T_0 \times D \]

where \( r(T) \) is the developmental rate; \( D \) is duration of development; \( T \) is the ambient temperature; \( T_0 \) is the lower and \( T_0 \) is the upper thermal limit; \( K \) is the thermal summation and \( \alpha \) is an empirical constant. Maximum developmental rate (\( T_m \)), was calculated analytically from the Briere model as (Briere et al. 1999, Dixon et al. 2009):

\[ T_m = \frac{2 \times m \times T_a + (m + 1) \times T_0 + \sqrt{4 \times m^2 \times T_a^2 + (m + 1)^2 \times T_0^2 - 4 \times m^2 \times T_a^2 \times T_a}}{4 \times m + 2} \]

for \( m = 2 \). Fitting was performed using nonlinear least squares procedure (Systat Software 2008).

The effect of temperature on survival of each life stage was described using an extreme-value distribution (Kim and Lee 2003, Son and Lewis 2005):

\[ S(T) = k \exp\left[1 + \frac{(T_{\text{max}} - T)}{\rho} - e^{\frac{(T_{\text{max}} - T)}{\rho}}\right] \]

where \( S(T) \) is the survival probability at temperature \( T \); \( k \) is the maximum survival rate; \( T_{\text{max}} \) is the temperature (°C) at which maximum survival occurs; and \( \rho \) is a fitted constant. The survival probability of a particular stage was calculated by dividing the initial number of individuals at each stage by the number of individuals who successfully developed to the next stage.

Females’ fecundity in relation to temperature was described via the Enkegaard model (Enkegaard 1993):

\[ F = (a + b \times x) \times e^{-c \times d} \]

where \( F \) is females’ fecundity, \( x \) is the days after emergence; \( a, b, c, d \) are estimated parameters. Moreover, the day when fecundity reaches the maximum at each examined temperature was analytically calculated as the parameter value for which the first derivative of Enkegaard’s model equals zero:

\[ x_{\text{max}} = \frac{a \times d - b}{b \times d} \]

All the analyses were conducted using SigmaPlot 11.0 (Systat Software 2008).

Results

Development and Survival of Immature Stages. P. quatuordecimpunctata completed development at all temperatures except 35°C, displaying temperature-dependent development (Table 1). The developmental time of total immature period decreased as temperature increased from 30.22 d (17°C) to 9.86 d (32.5°C). However, there was no difference in development.
Table 1. Duration of immature development in days (mean ± SE, median) of *P. quatuordecimpunctata* fed on *A. fabae* at different constant temperatures (no. in parentheses is the sample size)

| Stage of development | Temperature (°C) | First instar | Second instar | Third instar | Fourth instar | Pupa | Total immature period |
|----------------------|-----------------|--------------|---------------|--------------|---------------|------|-----------------------|
| Egg                  | 17.0            | 4.09 ± 0.21  | 3.89 ± 0.29   | 3.93 ± 0.28  | 3.86 ± 0.28   | 3.11 | 12.30 ± 0.24 (18)     |
|                     | 20.0            | 4.07 ± 0.21  | 3.89 ± 0.29   | 3.93 ± 0.28  | 3.86 ± 0.28   | 3.11 | 12.30 ± 0.24 (18)     |
|                     | 25.0            | 4.07 ± 0.21  | 3.89 ± 0.29   | 3.93 ± 0.28  | 3.86 ± 0.28   | 3.11 | 12.30 ± 0.24 (18)     |
|                     | 30.0            | 4.07 ± 0.21  | 3.89 ± 0.29   | 3.93 ± 0.28  | 3.86 ± 0.28   | 3.11 | 12.30 ± 0.24 (18)     |
|                     | 32.5            | 4.07 ± 0.21  | 3.89 ± 0.29   | 3.93 ± 0.28  | 3.86 ± 0.28   | 3.11 | 12.30 ± 0.24 (18)     |

Between 30 and 32.5°C, this trend was observed at each developmental stage. In particular, eggs required a mean time period for hatching from 6.24 d at 17°C to 1.78 at 32.5°C, where the mean duration of first, second, third, and fourth instars decreased from 4.04, 3.50, 3.11, and 5.16 d to 1.31, 0.93, 0.82, and 1.90 d at 17 and 32.5°C, respectively. Developmental time of pupa also decreased as temperature increased. Thus, it shortened from 8.37 to 3.10 d, at 17 and 32.5°C, respectively.

Temperature affected the survival of each developmental stage (excluding third instars) and total immature period (Table 2). For total immature period, survival decreased from 0.96 at 25°C to 0.14 at 32.5°C. At 25°C no mortality occurred among larval instars and pupa but some mortality occurred at the egg stage. In all instances, the lowest temperature examined (17°C) caused less mortality than the highest temperatures (32.5°C, 35°C).

**Modeling Developmental Rate and Survival.** Thermal summation and lower developmental threshold of *P. quatuordecimpunctata* total immature period were 218.0 degree days (DD) and 10.2°C. The lower developmental threshold ranged from 9.8°C for the pupa to 13.3°C for third instar larvae (Table 3). The estimations of Briere model for lower and upper developmental threshold for total immature period were 12.2 and 36.0°C, respectively. Temperature for maximum developmental rate was estimated at 30.3°C (Fig. 1).

Temperature-dependent survival (%) of *P. quatuordecimpunctata* (from egg to adult) was well described by the extreme value function ($R^2 = 0.99$; $F = 322.2$; df = 3, 5; $P = 0.0003$) (Fig. 2). The curve shows a skewed bell shape, indicating that survival decreases at both ends of the temperature range, but that higher temperatures have more detrimental impact than lower temperatures. The highest survival (94.8%) was estimated to occur at 24.6°C.

**Female Longevity and Fecundity.** Temperature also affected females’ longevity, which decreased from 123.06 d (17°C) to 33.53 d (30°C) (Table 4). The highest fecundity was recorded at 25°C (724.6 eggs/female). The Enkegaard model that was used to describe daily fecundity data gave a satisfactory fit at each temperature (Fig. 3). Maximum reproductive capacity occurred on 35th, 34th, 22nd, and 12th day at 17, 20, 25, and 30°C, respectively (Table 5).
Discussion

Our data suggest that immature development of *P. quatuordecimpunctata* would be seriously impaired under conditions of high temperature stress. Our study also showed that pupae are more sensitive than are eggs and larvae to temperature extremes. The

| Developmental stage | Briere | Ikemoto and Takai |
|---------------------|--------|-------------------|
|                     | $a$    | $T_0$ | $T_L$ | $T_m$ | $R^2$    | $K$  | $T_0$ | $R^2$ |
| Egg                 | 0.0005 ± 1.7862 × 10^{-5} | 13.8 ± 0.4 | 35.0 ± 4.218 × 10^{-5} | 29.8 | 0.855 | 36.5 ± 1.1 | 11.8 ± 0.3 | 0.950 |
| L1                  | 0.0006 ± 3.624 × 10^{-5}  | 13.1 ± 0.7 | 35.0 ± 6.139 × 10^{-5} | 29.7 | 0.733 | 26.9 ± 1.6 | 11.4 ± 0.5 | 0.827 |
| L2                  | 0.0009 ± 5.7589 × 10^{-5} | 14.6 ± 0.6 | 35.0 ± 7.196 × 10^{-5} | 29.9 | 0.701 | 18.8 ± 1.1 | 12.9 ± 0.5 | 0.896 |
| L3                  | 0.0012 ± 8.498 × 10^{-5}  | 14.7 ± 0.7 | 35.0 ± 8.374 × 10^{-5} | 29.9 | 0.635 | 15.1 ± 1.1 | 13.3 ± 0.5 | 0.859 |
| L4                  | 0.0005 ± 2.823 × 10^{-5}  | 12.5 ± 0.7 | 35.0 ± 5.948 × 10^{-5} | 29.6 | 0.746 | 34.6 ± 2.0 | 11.1 ± 0.6 | 0.830 |
| Pupa                | 0.0003 ± 1.249 × 10^{-5}  | 12.3 ± 0.6 | 35.0 ± 4.107 × 10^{-5} | 29.5 | 0.849 | 63.9 ± 2.7 | 9.8 ± 0.5  | 0.854 |
| Total immature      | $7.11 \times 10^{-5}$ ± $0.50 \times 10^{-5}$ | 12.2 ± 0.6 | $36.0 \pm 0.37$ | 30.3 | 0.837 | $218.0 \pm 5.0$ | $10.2 \pm 0.2$ | 0.961 |

*a* Parameter calculated analytically.

Fig. 1. Fitting of the Briere, and Ikemoto and Takai models to the observed developmental data of *P. quatuordecimpunctata* total immature period. Open circles are observed data and solid lines models’ prediction.
The effect of temperature on preimaginal developmental duration has been studied previously by Obrycki et al. (1993) and Honek and Kocourek (1988) studied the effect of temperature on the development of eggs and pupae. Our results are similar to those reported by Obrycki et al. (1993), for example, total immature developmental period at 30°C was 10.5 d for a population of *P. quatuordecimpunctata* from France and 10.6 d in our study. Additionally, the lower developmental threshold was 9.9°C in Obrycki et al. (1993) and 10.2°C in our study. However, here we describe detailed developmental times for each developmental stage that could be used in developing population dynamics models to project species establishment and performance (Gutiérrez et al. 2006). Honek (1996) stated that adaptations of insects' thermal requirements may occur primarily at the interspecific level. Earlier studies showed that geographical variation in intraspecific level did not affect coccinellid thermal responses (Obrycki and Tauber 1981, Miller 1992). Differences among studies may result from different source populations, different experimental protocols, or different statistical analyses.

Constant exposure to high temperatures was detrimental to the survival of all developmental stages of *P. quatuordecimpunctata*. We expect that mortality at these temperatures would decrease the abundance of the coccinellid. Adverse effects of high temperatures on survival and reproduction have also been reported for other coccinellid species (Xia et al. 1999, Grafton-Cardwell et al. 2005, Jalali et al. 2010). However, coccinellid species often avoid these influences by behavioral modifications such as migration to mountains for aestivation where temperatures are lower, although this is not demonstrated to occur in *P. quatuordecimpunctata* (Hodek and Honek 1996).

In nature, temperature changes during the course of each day. The pattern of exposure to temperatures affecting survival, development, and reproduction (Mironidis and Savopoulou-Soutiani 2008). Furthermore, short-term exposure to temperatures during the daily temperature cycle beyond the lower or higher thresholds may change mortality or development greatly.

The survival model described the relationship between constant temperature and survival for total developmental period adequately. The negative value of the parameter *p* indicates that *P. quatuordecimpunctata* has limited capabilities of survival at high temperatures. The developmental rate curve of *P. quatuordecimpunctata* by the nonlinear developmental model in relation to temperature is typical of insect development. Nonlinear models are more accurate at extreme temperatures, providing a better prediction for optimum temperatures as well.

The longevity of *P. quatuordecimpunctata* females showed an inverse response with increasing temperature in the temperature range of the study. In coccinellids, as in all ectotherms, it is generally accepted

**Table 4.** Mean fecundity (eggs/female) and longevity (days) of *P. quatuordecimpunctata* adult females at different constant temperatures (prey was *A. fabae*).

| Temperature (°C) | n  | Fecundity Mean ± SE | Median | Longevity Mean ± SE | Median |
|-----------------|----|---------------------|--------|--------------------|--------|
| 17              | 16 | 371.61 ± 67.57      | 347b   | 123.06 ± 10.63     | 115.0a  |
| 20              | 20 | 539.00 ± 51.62      | 553ab  | 118.20 ± 7.96      | 116.5a  |
| 25              | 25 | 724.61 ± 47.33      | 712a   | 69.04 ± 3.1        | 71.0b   |
| 30              | 15 | 402.30 ± 49.19      | 373b   | 33.53 ± 1.87       | 34.0c   |
| *H*             |    | 53.95               | 17.45  |                    |        |
| df              |    | 3                   | 3      |                    |        |
| *P*             |    | <0.001              | <0.001 |                    |        |

Medians within a column followed by the same letter are not statistically different (Kruskal-Wallis analysis of variance on ranks; Dunn test *α* = 0.05).
that life span shortens with increasing temperature because of the acceleration of biological processes (Hodek and Honěk 1996). Females were able to oviposit more eggs at 25°C, whereas reproductive capacity did not differ between 17, 20, and 30°C. This was because, at 30°C, despite reduced longevity, females laid more eggs each day.

The emergence, development, and seasonal abundance of species in given habitats are strongly related to their thermal summation and thermal thresholds. As temperature increases above the lower developmental threshold, insects need less time to complete specific developmental requirements in a viable temperature range. This time-period reaches a minimum value at the optimum temperature and therefore rapid off-spring development leads to an additional increase of the population until rising temperature cause substantial mortality. Therefore, the knowledge of thermal summation is useful for the prediction of the coccinellid’s phenology. However, a coccinellid’s phenology is affected not only by temperature. Photoperiod, food abundance, temperature, and their interaction play important roles as well (Hodek and Honěk 1996).

A careful analysis of how predator–prey systems respond to abiotic factors such as temperature is required for successful management decisions. Integration of mainly temperature-driven models to simulate population dynamics of herbivores and their natural enemies has been developed that predicts the species dynamics and interactions in a wide geographic area (Gutiérrez et al. 2006). The information presented in this article forms the basis for developing a more complete understanding of $P.\ quatuordecimpunctata$ development. Our data will be useful in creating a temperature-based degree-day model for predicting the occurrence of key life stages in the field.

The impact of developmental thresholds, as well as the thermal summation, is well recognized from biological control practitioners (Messenger 1959, Jervis and Copland 1996). The probability of the establishment of a biological control agent increases if the climate conditions in the release area are similar to those that the agent is adapted to. In addition, these parameters are useful tools for the prediction of the phenology of an insect pest and/or its natural enemy, as coexistence of a predator and its prey in field conditions is often desirable.

Acknowledgments

This manuscript is a part of N. Papanikolaou’s Ph.D. thesis. The comments by three anonymous reviewers are greatly appreciated. We would also like to thank D. Papachristos for comments and discussions on coccinellids and K. Prescott for language editing and comments on the manuscript. This study was partially funded by Benaki Phytopathological Institute.

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Received 19 August 2012; accepted 30 November 2012.