Temperature is a key factor affecting the performance of insects, playing a part in determining primary biological features such as survival and reproductive rates (Milonas and Savopoulou-Soutmani 2000, Kontodimas et al. 2007, Jalali et al. 2009, Papanikolaou et al. 2013). As a consequence, temperature is a critical aspect of insects’ population dynamics, regulating their growth rate and allowing for population fluctuations through time. Typically, growth increases with temperature up to a maximum or optimal degree and then declines as temperature approaches damaging levels. A life table analysis provides the basis for elucidating fitness components of an organism and how they fluctuate with abiotic factors. Tabulating the survivorship and fecundity schedules of individuals from birth to death is fundamental for cohort life tables (Carey 1993). This enables the calculation of several parameters that allow the prediction of insects’ performance, as well as an investigation of mortality and reproduction patterns. A common estimate of population fitness is the Malthusian parameter, that is, the intrinsic rate of increase, generation time, and doubling time was detected. Estimated values of intrinsic rate of increase were 0.065, 0.095, 0.166, and 0.190 females per female per day at 17, 20, 25, and 30°C, respectively, where Lactin model indicated that the maximum value is achieved at 29.23°C. Females of ≈75, 50, 45, and 20 d old reach their maximum reproductive potential at 17, 20, 25, and 30°C, respectively. In addition, temperature affected the risk of death of immature and female adults, as the survival curves at the examined temperatures were significantly different. The mean survival times decreased from 19.9 to 8.0 d and 123.1 to 33.5 d from 17 to 30°C for entire immature stages and female adults, respectively.

KEY WORDS Coccinellidae, intrinsic rate of increase, life table, survival curve

Predaceous Coccinellidae species have received much attention from biological control workers for over a century (Dixon 2000). They prey mainly on aphids and coccids, where they show remarkable predation efficiency (Obrycki and Kring 1998). A Paleartic aphidophagous coccinellid, which has also been established in the Nearctic region (Wheeler 1990), is the 14-spotted ladybird beetle, Propylea quatuordecimpunctata L. (Coleoptera: Coccinellidae). Kalushkov and Hodek (2005) reported up to 20 aphid species as possible food for this predator, including the bean aphid, Aphis fabae Scopoli (Hemiptera: Aphididae). Recently, Papanikolaou et al. (2013) reported detailed information on the effect of temperature on the development, survival, longevity, and fecundity of P. quatuordecimpunctata reared on A. fabae. Here, we focus on demographic analyses and life table statistics of P. quatuordecimpunctata to provide further information on its performance under a broad temperature range.

Materials and Methods

Insects. The coccinellid was collected in the summer of 2006 from corn, Zea mays L., plants infested by the corn leaf aphid, Rhopalosiphum maidis Fitch, in Arta County (northwestern Greece, 21°0’0”, 39°10’0”) and was reared for four generations on A. fabae infesting potted fava bean, Vicia faba L., plants at 25 ± 1°C, 65 ± 2% relative humidity (RH), and a photoperiod of 16:8 (L:D) h in large cylindrical Plexiglas cages (50 by 30 cm). Before conducting the experiment, a P. quatuordecimpunctata colony was reared for two gen-
erations at each of the temperature treatments. An *A. fabae* colony originally from a stock colony at the Biological Control Laboratory, Benaki Phytopathological Institute, Kifissia, Greece, was reared on *V. faba* plants at 20 ± 1°C (65 ± 2% RH and a photoperiod of 16:8 (LD) h).

**Life Table Parameters.** Using data on development, survival, fecundity, and longevity of *P. quatuordecimpunctata* of an earlier study by Papanikolaou et al. (2013), the following parameters were calculated at 17, 20, 25, and 30 ± 1°C, 65 ± 2% RH, and a photoperiod of 16:8 (LD) h (Kontodimas et al. 2007, Borges et al. 2012): the cohort survival to age *x*, the age-specific mortality, the age-specific fecundity by multiplying the mean number of eggs by the ratio *g* / (*g* + *δ*) (observed by sorting 150–200 offsprings), the net reproductive rate, the intrinsic rate of increase, the finite rate of increase, the mean generation time, the doubling time, the reproductive value of the females, and the expected remaining lifetime of the females. Significant differences between life table parameters at each of the examined temperature were tested with the superposition of 95% CIs (Wald test), which were obtained by bootstrapping in R (R Development Core Team 2010). In particular, for each treatment, we sampled 10,000 individuals to derive 95% CIs, which do not rely on asymptotic normality.

**Modeling Temperature-Dependent Intrinsic Rate of Increase.** The relationship between temperature and the intrinsic rate of increase was described by the Lactin model (Lactin et al. 1995), which is of the form:

\[ r(T) = e^{\psi \times T} - e^{\psi \times T_m - \frac{T_m - T}{\Delta}} + \lambda, \]

where *T* is the ambient temperature; *ρ* represents the steepness of increase in the intrinsic rate of increase; *Δ* is the width of the high temperature boundary layer; *λ* is the intersection of the fitted model curve with abscissa at the lower temperatures; *T_m* is an estimated parameter. The temperature at which the intrinsic rate of increase reaches its maximum value (*T_{m_{op}}*) was calculated analytically as the parameter value for which Lactin model’s first derivative equals zero:

\[ T_{opt} = \frac{\ln(\rho \times \Delta) - \rho \times T_m + \frac{T_m}{\Delta}}{\frac{1}{\Delta} - \rho}, \]

Fitting was performed using a nonlinear least squares procedure (Systat Software 2008).

**Survival Analysis.** The Kaplan-Meier method was used to estimate the survival curves for entire immature stages and females at each of the examined temperatures. As the log rank test indicated that survival curves were significantly different, we used the Holm-Sidak test to determine which pairs of curves were different. The Kaplan-Meier estimate was used to obtain mean survival times and their 95% CIs.

**Results**

**Life Table Parameters.** The estimated life table parameters showed a variation across the temperature regimes used in this study, based on the superposition of 95% CIs criterion (Table 1). The net reproductive rate increased from 90.2 females per female at 17°C to 375.1 at 25°C, followed by a decrease to 81.1 at 30°C. A decreasing trend was determined for the values of the intrinsic and the finite rate of increase as temperature increased from 17°C (0.065 females per female per day and 1.07, respectively) to 30°C (0.190 females per female per day and 1.21, respectively). An inverse relationship of temperature to mean generation time (69.5 d at 17°C and 23.1 d at 30°C) and doubling time (10.7 d at 17°C and 3.6 d at 30°C) was detected, based on the estimated 95% CIs.

The age-specific fecundity, as well as the reproductive value and the expected remaining lifetime, increased until a particular age depending on temperature, where an ultimate decrease followed (Figs. 1 and 2). In contrast, the age-specific mortality showed a U-shaped trajectory (Fig. 3).

**Temperature-Dependent Intrinsic Rate of Increase.** The Lactin model fitted the estimated parameters of *P. quatuordecimpunctata* intrinsic rate of increase related to temperature efficiently (*R^2* = 0.9977; Fig. 4). The model’s prediction indicates that the intrinsic rate of increase reaches its maximum value at 29.23°C.

**Survival Analysis.** Temperature also affected the risk of death of immature (*χ^2* [Log rank] = 34.108; df = 3; *P* < 0.001) and female adults (*χ^2* [Log rank] = 147.021; df = 3; *P* < 0.001; Fig. 5). Moreover, *P. quatuordecimpunctata* mean survival times for entire immature stages and females decreased with temperature increase (Table 2). Thereby, the survival time for entire immature stages decreased from 19.9 d at 17°C to 8.0 d at 30°C, where the respective values for the females were 123.1 and 33.5 d.
This study provides a comprehensive description of the survival and reproductive schedules of *P. quatuordecimpunctata* in the laboratory. It also provides further knowledge on coccinellid’s growth rate, allowing for potential application in biological control practice. The selection and release of candidate biological control agents are usually based on their comparative values of the intrinsic rate of increase (Gutierrez 1996, Kontodimas et al. 2008). Furthermore, a key characteristic of predators as biological control agents is the ratio of generation time of a predator to that of its prey. Generally, the longer the generation time ratio, the smaller the degree of prey depletion (Kindlmann and Dixon 1999, 2001). In addition, biological features of *P. quatuordecimpunctata* may be incorporated in prey-predator models evaluating the population dynamics of the study organisms, or mass-rearing models allowing for efficient coccinellid breeding in the insectary (Carey and Vargas 1985).

Our study also demonstrates that there is a significant variation of the population parameters of *P. quatuordecimpunctata* at the viable temperature range that the coccinellid can grow and reproduce. The Lactin model indicates that *P. quatuordecimpunctata* intrinsic rate of increase shows an increasing tendency until 29.23°C, where it reaches the maximum value. The
subsequent decrease at higher temperatures is because of the determinant effect of these temperatures on predator’s survival (Papanikolaou et al. 2013). According to our study, temperatures around 30°C are optimal for population growth of the coccinellid. In general, Propylea species show competitive values of intrinsic rate of increase compared with other coccinellids (Kontodimas et al. 2008, Pervez and Omkar 2011). This may be a reason that invasions of Harmonia axyridis (Pallas) (Coleoptera: Coccinellidae) did not reduce the abundance of P. quatuordecimpunctata in North America (Pervez and Omkar 2011). However, a study on population parameters of Hippodamia variegata Goeze reared on A. fabae by Forhadi et al. (2011) reported a higher value of coccinellid’s intrinsic rate of increase.

Obrycki et al. (1993) studied three different populations of P. quatuordecimpunctata reared on Acyrthosiphon pisum (Harris) at 26°C, where the coccinellid showed similar values of intrinsic and finite rate of increase (0.14–0.15 and 1.1–1.2, respectively) compared with our results at a similar temperature (25°C). In addition, the net reproductive value was significantly different (148.9–189.5), probably because of different aphid species and host plants used in the study. Literature suggests that there is variation in insects’ life table characteristics resulting from the provided diets or prey’s plant host (e.g., Wang et al. 2008, Jalali et al. 2009, Papachristos and Papadopoulos 2009).

Our results also showed that temperature affects the survival probabilities of both immature stages and P. quatuordecimpunctata adult females. Moreover, mortality risk of immature stages is decreased during their lifetime, which is followed by an increase during coccinellid’s reproductive life span. A U-shaped trajectory in mortality experience is common in insects, by a trough formed between youngest stages and the reproductive adults (Carey 2001). This trait is reflected to the expected remaining lifetime.

The reproductive value of females, that is, the contribution an individual age $x$ will make to the future generation (Carey 1993), increases until a specific age. This is because of the early mortality of the prereproductive age classes of P. quatuordecimpunctata and the subsequent increase of the age-specific fecundity. Thereafter, a decrease to the age-specific fecundity has a negative effect on the reproductive value, which declines to zero for the older ages. Individuals of roughly 75, 50, 45, and 20 d old at 17, 20, 25, and 30°C,

**Table 2. Mean survival times (95% CIs) of the entire immature stages and females of P. quatuordecimpunctata at constant temperatures obtained from Kaplan-Meyer method**

| Temp (°C) | Entire immature stages (d) | Females (d) |
|----------|---------------------------|-------------|
| 17       | 19.9 (16.1–23.8)          | 123.1 (102.2–143.9) |
| 20       | 19.7 (16.5–22.6)          | 118.2 (102.8–133.6) |
| 25       | 17.0 (—)                  | 69.0 (63.0–75.3)   |
| 30       | 8.0 (6.6–9.4)             | 33.5 (30.0–37.2)   |
respectively, exude their maximum reproductive potential, ideal for release in biological control practice.

Concluding, we expect that environmental stochasticity may lead life history parameters of *P. quatuordecimpunctata* to several fluctuations. However, the results of this study are indicative of this coccinellid’s performance over a broad temperature range. A further knowledge of the numerical response of the predator, that is, a change in predator density caused by a change in prey abundance (Crawley 1975), could be desirable to group together more information on the system’s population dynamics.

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