ORIGINAL ARTICLE

Modeling temperature-dependent development and demography of *Adalia decempunctata* L. (Coleoptera: Coccinellidae) reared on *Aphis gossypii* (Glover) (Homoptera: Aphididae)

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Abstract

Development and demography of *Adalia decempunctata* L. were studied under laboratory conditions at seven constant temperatures (12, 16, 20, 24, 28, 32 and 36°C). First instar larvae failed to develop to second instar at 12°C and no development occurred at 36°C. The total developmental time varied from 47.92 days at 16°C to 15.94 days at 28°C and increased at 32°C. The lower temperature thresholds of 11.05 and 9.90°C, and thermal constants of 290.84 day-degree and 326.34 day-degree were estimated by traditional and Ikemoto-Takai linear models, respectively. The lower temperature threshold (T_{min}) values estimated by Analytis, Briere-1, Briere-2 and Lactin-2 for total immature stages were 11.99, 12.24, 10.30 and 10.8°C, respectively. The estimated fastest developmental temperatures (T_{fast}) by the Analytis, Briere-1, Briere-2 and Lactin-2 for overall immature stages development of *A. decempunctata* were 31.5, 31.1, 30.7 and 31.7°C, respectively. Analytis, Briere-1, Briere-2 and Lactin-2 measured the upper temperature threshold (T_{max}) at 33.14, 36.65, 32.75 and 32.61°C. The age-stage specific survival rate (s_{xj}) curves clearly depicted the highest and lowest survival rates at 16 and 32°C for males and females. The age-specific fecundity (m_x) curves revealed higher fecundity rate when fed *A. gossypii* at 24 and 28°C. The highest and lowest values of intrinsic rate of increase (r) were observed at 28 and 16°C (0.1945 d^{-1} and 0.0592 d^{-1}, respectively). Also, the trend of changes in the finite rate of increase (λ) was analogous with intrinsic rate of increase. The longest and shortest mean generation time (T) was observed at 16 and 28°C, respectively and the highest net reproductive rates (R_0) was estimated at 24 and 28°C. According to the results, the most suitable temperature seems to be 28°C due to the shortest developmental time, highest survival rate, and highest intrinsic rate of increase.

Keywords: *Aphis gossypii*, Coccinellidae, Integrated Pest Management (IPM), thermal model

Introduction

Temperature is considered to be one of the most important abiotic factors which affects the developmental rate, biological traits, and population growth parameters of pests and their natural enemies (Wagner *et al.* 1984; Huffaker and Gutierrez 1999; Roy *et al.* 2002). Therefore, it seems to be a prerequisite to measure the critical

temperatures (low and high thresholds) and also the optimal temperature for different life stages of any pest as well as its natural enemies (Wagner *et al.* 1984; Huffaker and Gutierrez 1999). Insects only develop within a temperature range between low and high thresholds, and their development stops at temperatures below the lower threshold or above the higher threshold. Linear and nonlinear models have been developed to describe the relationship between temperature and development in order to estimate the thresholds across various insect species (Campbell *et al.* 1974; Wagner *et al.* 1984; Lamb 1992; Lactin *et al.* 1995; Briere *et al.* 1999). Linear models help researchers evaluate two parameters, including a lower temperature threshold (at which developmental rate would be zero) and the sum of effective temperature (SET), which is defined as the thermal constant required to complete a special stage (Jalali *et al.* 2010). The developmental rate is zero at lower temperature thresholds, but it gradually increases to the highest level by elevating the temperature up to the optimum. It then rapidly diminishes by the temperature increment at high thresholds (Wagner *et al.* 1984). The nonlinear models represent a relationship between temperature and developmental rate in a wider temperature range. They also estimate the maximal and optimal temperatures for growth but are unable to evaluate SET (Jarosik *et al.* 2002; Kontodimas *et al.* 2004).

The intrinsic rate of increase (*r*) can be used to estimate the ability of natural enemies in leveling up their population on the target host (Force and Massenger 1968; Kambhampati and Mackauer 1989; Southwood and Handerson 2009). Amarasekare and Savage (2012) demonstrated that the temperature, at which the highest *r* value occurs, must be regarded as the optimal temperature. A temperature based insect developmental growth rate would be useful for determining the number of generations and predicting the life cycle (Wagner *et al.* 1984). Forecasting is regarded as a strategy for integrated pest management (IPM) (Wagner *et al.* 1984; Haghani *et al.* 2007). Thermal models concentrating on natural enemies could be helpful to determine the optimal conditions for mass rearing in biological control projects (Rodriguez–Saona and Miller 1999). This knowledge is useful for selecting a proper natural enemy for target pests with the best available conditions (Rosen and Huffaker 1983; Obrycki and Kring 1998). Thus, in biological control programs, when the responses of natural enemies to climatic factors including temperature are known, the control of pests could be facilitated (Roy *et al.* 2002). Several studies have focused on temperature as one of the most important factors, which influences development, reproduction, and thus have helped to estimate critical temperatures and thermal requirements in some coccinellid predators (e.g. Obrycki and Tauber 1978, 1982;

Miller 1992; Miller and LaMana 1996; Rodriguez-Saona and Miller 1999; Rebolledol *et al.* 2009; Jalali *et al.* 2009; Jalali *et al.* 2010; Papanikolaou *et al.* 2013).

Adalia decempunctata L. is a common Palaearctic species found in Europe, East Asia, and North Africa (Hodek 1973; Nikitsky and Ukrainsky 2016). It is often known as an aphidophagous ladybeetle (Nikitsky and Ukrainsky 2016). Predation of larvae and adult insects have been reported from numerous trees such as *Mulus* sp. (Hodek 1973), *Prunus* sp. (Honek 1985; Guncan and Yoldas 2010), *Citrus* sp. (Magro *et al.* 1999) *Castanea* sp. (Santos *et al.* 2012), *Acer* sp., *Betula* sp. and *Tilia* sp. infected by aphids (Honek 1985; Honek *et al.* 2016).

Little research has been done on biological traits and thermal requirements of *A. decempunctata* (Hodek 1973; Mojib *et al.* 2018). Hence, the current knowledge about *A. decempunctata* seems to be insufficient, and requires more attention. We are certain that the present study will enhance our understanding and simulate this predators' behavior in natural environments. Therefore, our aim was to investigate the effects of seven constant temperatures (i.e. 12, 16, 20, 24, 28, 32 and 36°C) on biological traits and developmental parameters, in order to determine the critical temperatures in *A. decempunctata* feeding on *Aphis gossypii* (Glover) using linear and nonlinear models.

Materials and Methods

Rearing of *Aphis gossypii* and *Adalia decempunctata*

Cucumber seeds (*Cucumis sativus* L. var. Beith Alpha) were individually planted in containers (20-cm in diameter) under controlled greenhouse conditions set at 24 ± 4°C, 70 ± 10% relative humidity (RH), and a photoperiod of 14 : 10 h (L : D). In early spring, adults of *A. gossypii* were collected from cucumber farms in Pirbazar located in Rasht, Guilan province, Iran (37°21'16.08" N, 49°25'54.72" E) and were released on the plants in the greenhouse. In order to have a cohort of aphids, adults (*n* = 100) were transferred onto healthy plants and were allowed to produce nymphs for 24 h. Then, the adults were removed and the nymphs developed until adult stage. The aphid colony was maintained by transferring healthy plants to the greenhouse on a weekly basis. *Aphis gossypii* is a major pest of citrus trees and is particularly important for the transmission of plant viruses (Komazaki 1994). Therefore, this aphid was selected in order to simulate a natural diet for *A. decempunctata*.

In order to initiate an *A. decempunctata* colony, the adults were originally collected from pomegranate trees infested with *A. punicae* Passerini by shaking

the branches over a white tray during the spring. Then, they were placed in transparent $12 \times 10 \times 6$ cm^3 plastic culture containers. A circular hole 3 cm in diameter was made on the lid and covered with a piece of mesh for ventilation. The jars were maintained in a growth chamber (Model: SG60018, Paradise, Iran) set at $24 \pm 1°C$, $65 \pm 5\%$ RH and 16 : 8 h (L : D) photoperiod. Egg clusters obtained from this population were separately reared on *A. gossypii*, and the insects born from these eggs were used to initiate the colony in the laboratory.

Developmental and life table parameters of *Adalia decempunctata* at different temperatures

For each temperature treatment, 100 eggs (<24 h old) obtained from 10–15 pairs of *A. decempunctata* were kept individually in groups in Petri dishes (8 cm in diameter) and reared at an assigned temperature but all at $65 \pm 5\%$ RH, and a photoperiod of 16 : 8 h (L : D). The incubation period was recorded and one-day-old larvae were individually transferred to $8 \times 6 \times 4$ cm^3 plastic containers. Each larva was reared on prey (third instar nymphs of *A. gossypii*) until pupation. Newly emerged adults were transferred to Petri dishes (10 cm in diameter) for mating. The mated insects were placed in new containers ($12 \times 10 \times 6$ cm^3) containing prey (third and fourth instar nymphs of *A. gossypii*) and their oviposition was recorded. Observations were made daily, until the death of each female and male.

Mathematical models

Two linear models and four nonlinear models were used to determine the relationship between temperature and developmental rate of *A. decempunctata*. Linear models are commonly used to evaluate thermal constants and lower temperature thresholds. Due to their deviation from linearity, the developmental rates of eggs, larvae, pupae, and all immature stages of *A. decempunctata* were disregarded at 32°C.

Traditional linear model:

$$r\ (T)\ \text{or}\ \frac{1}{D} = a + (b \times T),$$

where: r – the rate of development, D – duration of development (days) at temperature T, a – the intercept, b – the slope of the linear function (Campbell *et al.* 1974; Obrycki and Tauber 1982; Jarosik *et al.* 2002).

Ikemoto and Takai linear model:

$$DT = K + T_{min}\ D,$$

where: D – the developmental duration (days), T – the ambient temperature, T_{min} – the lower temperature threshold and K – the thermal constant (Ikemoto and Takai 2000).

The relationship between temparature and developmental rate was not linear near high or low thresholds. Therefore, four nonlinear models (Analytis, Briere-1, Briere-2 and Lactin-2) were used to determine the developmental rate within a wide range of temperatures. The nonlinear models were calculated according to the following formulae:

Briere-1 model (Briere *et al.* 1999):

$$\frac{1}{D} = a \times T(T - T_{min}) \times (T_{max} - T)^{1/2},$$

Briere-2 model (Briere *et al.* 1999):

$$\frac{1}{D} = a \times T(T - T_{min}) \times (T_{max} - T)^{1/n},$$

Lactin-2 model (Lactin *et al.* 1995):

$$\frac{1}{D} = \exp(p \times T) - \exp\left(p \times T_{max} - \left(\frac{T_{max} - T}{\Delta T}\right)\right) + \lambda,$$

Analytis model (Analytis 1981)

$$\frac{1}{D} = a \times (T - T_{min})^n \times (T_{max} - T)^m,$$

where: D – duration of development (days), T_{min} – the lower temperature threshold, T_{max} – the upper temperature threshold, a, d, m, n, p, λ and Δ – the constant coefficients for the model's suitability (Analytis 1981; Briere *et al.* 1999; Roy *et al.* 2002; Kontodimas *et al.* 2004).

The accuracy of the linear models was evaluated based on the statistical indices including: R^2 (coefficients of determination) and R^2_{adj} (adjusted coefficients of determination). R^2_{adj} and Akaike informaton criterion (*AIC*) were also used to evaluate the nonlinear models. The higher value of the R^2_{adj} and lower value of the *AIC* suggest a high accuracy level of the model (Akaike 1974). *AIC* parameter was calculated by the following formula (Vucetich *et al.* 2002):

$$AIC = n \ln\left(\frac{SSE}{n}\right) + 2p,$$

where: n – the number of observations, p – the number of the parameters, *SSE* – the sum of squared errors.

The following indices were used for each of the noted models:

Lower temperature threshold (T_{min}) is defined as the temperature at which no development occurs (the developmental rate is zero). Lower temperature threshold

has been estimated as the intercept of the development curve with the temperature axis (Campbell *et al.* 1974). This temperature can also be calculated by the linear model and some of the nonlinear models. The standard error for the linear model is calculated by the following formula:

$$SE_{T_{min}} = \frac{\bar{r}}{b} \sqrt{\frac{s^2}{N\bar{r}^2} + \left[\frac{SE_b}{b}\right]^2},$$

where: $SE_{T_{min}}$ – the standard error of low temperature (T_{min}) for the linear model, s^2 – the residual mean square of r, $\bar{r}$ – the sample means, SE_b – the standard error, b – the slope of the linear function, N – the number of the samples (Campbell *et al.* 1974; Kontodimas *et al.* 2004).

Upper temperature threshold (T_{max}) is the first maximum temperature at which the developmental rate is zero or life cannot be sustained for a long time. This temperature can be calculated by a nonlinear model (Kontodimas *et al.* 2004).

Fastest developmental temperature (T_{fast}) is when the developmental rate reaches maximum at the fastest developmental temperature. It may be calculated directly from some of the nonlinear models (Kontodimas *et al.* 2004).

Thermal constant (K) is the amount of thermal energy (day-degree, *DD*) which is needed to complete a stage of the insect's development which can only be calculated by a linear model. The value of *SE* for *K* is calculated using the following formula (Campbell *et al.* 1974; Kontodimas *et al.* 2004):

$$SE_K = \frac{SE_b}{b^2},$$

where: SE_K – the standard error of K, SE_b – the standard error of b, b – the slope of the linear function.

Statistical analysis

The life table data of all individuals (including males, females, and those not reaching the adult stage) were analyzed using the age-stage, two-sex life table theory (Chi and Liu 1985) and the method described by (Chi 1988). Data analysis and population parameters were calculated using the TWOSEX-MSChart computer program (Chi 2018). The age-stage specific survival rate (s_{xj}) (x – age and j – stage), the age-stage-specific life expectancy (e_{xj}), the age-specific survival rate (l_x), the age-specific fecundity (m_x), the population indices, the intrinsic rate of increase (r), the finite rate of increase (λ), the net reproductive rate (R_0), and the mean generation time (T) were calculated accordingly (Chi and Liu 1985). The means and *SEs* of biological traits and life table parameters were estimated by the bootstrap procedure with 10,000 resamplings. A paired

bootstrap test procedure was used to capture the differences between treatments based on the confidence interval of differences (Chi 2018). The statistical software SigmaPlot ver. 12.0 was used for drawing all the figures (Polat-Akköprü *et al.* 2015). While determining the effects of temperature on the developmental period of *A. decempunctata*, the development stopped in the first instar larvae and egg stages at 12 and 36°C, respectively. Therefore, the recorded data were removed from thermal requirement evaluations. The nonlinear analysis was calculated by JMP v.7.0 software (SAS Institute, 2007) and all the diagrams were drawn by Excel v. 2010.

Results

Developmental time

Table 1 provides the means of developmental times for different immature stages of *A. decempunctata* at seven constant temperatures.

The results demonstrated that all immature stages of *A. decempunctata* were able to complete their development within a temperature range of 16 to 32°C. According to our results, the eggs hatched at 12°C with a 21% survival rate. Neonate larvae developed into second instar larvae with a 19.04% survival rate, though these larvae were unable to survive. None of the eggs hatched at 36°C. Comparison of the means by the bootstrap method showed that the temperature had a significant effect on developmental periods of the predator egg, pupal and immature stages ($p < 0.05$). With the temperature rising from 16 to 28°C, developmental times significantly decreased. However, with an elevation of temperature from 28 to 32°C, the total developmental time slightly increased (from 15.94 to 17.82 days) (Table 1). Moreover, the numbers of emerged adults were 39, 44, 53, 69 and 44 at 16, 20, 24, 28 and 32°C, respectively. The survival rates of different stages of *A. decempunctata* showed the minimum value at 16°C with 39%, while the highest survival rate was 69% at 28°C (Table 1).

Evaluation of models

The coefficients of determination (R^2_{adj}, R^2), T_{min}, and K parameters estimated for linear models (traditional and Ikomoto-Takai) are provided in Table 2. The developmental rate of *A. decempunctata* increased linearly within the temperature range of 16 to 28°C. The developmental data at 32°C was eliminated from linear regression due to deviation from linearity. Based on traditional and Ikomoto-Takai linear models, *A. decempunctata* needed 290.84 ± 20.53 and 326.34 ± 47.71 *DD* to develop from egg into adult over T_{min} of 11.05 ± 1.06 and 9.90 ± 1.22°C, respectively (Table 2). Figure 1 demonstrates the relationship between

Table 1. Comparative duration (mean ± SE) of immature stages (days) of *Adalia decempunctata* at seven constant temperatures fed *Aphis gossypii*

Stages	Temperature [ºC]						
	12	16	20	24	28	32	36
Egg	10.37 ± 0.2	6.58 ± 0.15 a	4.83 ± 0.08 b	3.01 ± 0.09 c	2.46 ± 0.08 d	2.65 ± 0.09 d	–
No(s)	100(21)	100(79)	100(81)	100(91)	100(92)	100(85)	
Instar I	6.5 ± 0.2	5.57 ± 0.16 a	4.28 ± 0.12 b	3.77 ± 0.110 c	1.88 ± 0.09 d	2.08 ± 0.12 d	–
No(s)	21(19.04)	79(79.74)	81(82.71)	91(89.01)	92(91.30)	85(85.88)	
Instar II	–	6.02 ± 0.13 a	5.20 ± 0.14 b	3.44 ± 0.11 c	2.14 ± 0.09 d	2.05 ± 0.11 d	–
No(s)		63(88.88)	67(89.65)	81(86.41)	84(92.85)	73(90.41)	
Instar III	–	5.07 ± 0.13 a	3.0 ± 0.1 b	2.63 ± 0.08 c	1.40 ± 0.07 d	1.49 ± 0.10 d	–
No(s)		56(89.28)	60(91.66)	70(88.57)	78(94.87)	66(86.36)	
Instar IV	–	11.09 ± 0.22 a	8.02 ± 0.17 b	5.94 ± 0.11 c	3.83 ± 0.09 d	4.29 ± 0.18 e	–
No(s)		50(92)	55(90.90)	62(91.93)	74(97.29)	57(89.47)	
Prepupa	–	2.69 ± 0.09 a	2.50 ± 0.10 a	1.55 ± 0.07 b	1.04 ± 0.02 c	1.14 ± 0.05 c	–
No(s)		46(93.47)	50(92)	57(94.73)	72(100)	51(96.07)	
Pupa	–	10.85 ± 0.31 a	7.98 ± 0.17 b	5.40 ± 0.14 c	3.30 ± 0.08 d	3.66 ± 0.15 e	–
No(s)		43(90.69)	46(95.65)	54(96.29)	72(95.83)	49(89.79)	
Overall immature	–	47.92 ± 0.69 a	36.02 ± 0.54 b	25.90 ± 0.35 c	15.94 ± 0.23 d	17.82 ± 0.38 e	–
No(s)		100(39)	100(44)	100(53)	100(69)	100(44)	

No – sample size; s – survival (%). Mean values in each row followed by the same letter are not significantly different (paired bootstrap test at 5% level)

Table 2. The regression equations, lower temperature threshold (T_{min} ± SE) and thermal constant (K ± SE) estimated by linear models for immature stages of *Adalia decempunctata*

Stage	Regression	T_{min}	K	R^2	R^2_{adj}	P
		Traditional model				
Egg	1/D = 0.2842 + 0.0265T	10.72 ± 1.25	40.44 ± 1.90	0.972	0.959	0.014
Larvae	1/D = 0.0059 + 0.0656T	11.11 ± 1.88	156.23 ± 13.74	0.899	0.849	0.042
Pupa	1/D = 0.018 + 0.213T	11.82 ± 0.48	57.38 ± 4.40	0.929	0.894	0.036
Pre-adult	1/D = 0.2842 + 0.0265T	11.05 ± 1.06	290.84 ± 20.53	0.925	0.887	0.038
		Ikemoto-Takai model				
Egg	DT = 45.91 + 9.422D	9.422 ± 1.3	45.91 ± 5.93	0.962	0.943	0.065
Larvae	DT = 195.98 + 9.65D	9.65 ± 1.5	195.98 ± 50.30	0.874	0.812	0.014
Pupa	DT = 65.43 + 10.65D	10.65 ± 1.96	65.43 ± 14.63	0.936	0.904	0.033
Pre-adult	DT = 326.34 + 9.9D	9.90 ± 1.22	326.34 ± 47.71	0.909	0.863	0.047

D – the developmental duration (days); T – the ambient temperature (°C); DT – development (day) × temperature (°C); T_{min} – the lower temperature threshold; K – the thermal constant; R^2 – coefficient of determination; R^2_{adj} – adjusted coefficient of determination, P – probability value

temperature and developmental rate based on the two linear models.

The data for the developmental rate of the egg, larva, pupa and total immature stages were fitted by four nonlinear models including Analytis, Briere-1, Briere-2 and Lactin-2 within a temperature range of 16 to 32°C (Table 3, Fig. 2). The R^2_{adj} in the overall immature period was estimated as 0.8963, 0.9036, 0.9310, and 0.9277 for Analytis, Briere-1, Briere-2, and Lactin-2, respectively. Figure 2 illustrates the correlation curves between temperature and developmental rate relative to the overall immature period calculated by the mentioned models. The lower threshold temperatures for pre-adult stages were estimated as 11.99, 12.24, 10.30 and 10.8 in Analytis, Briere-1, Briere-2 and

Lactin-2, respectively. Our results also demonstrated that the T_{fast} values for overall immature stages were 31.5, 31.1, 30.7 and 31.7°C in Analytis, Briere-1, Briere-2, and Lactin-2, respectively. T_{fast} is the temperature at which developmental time is the shortest. However, the fitness of the population might not be maximal due to the high mortality. In addition, T_{max} for total immature stages of *A. decempunctata* was recorded as 33.14°C for Analytis, 36.65°C for Briere-1, 32.75°C for Briere-2 and 32.61°C for Lactin-2.

Survival, life expectancy and fecundity

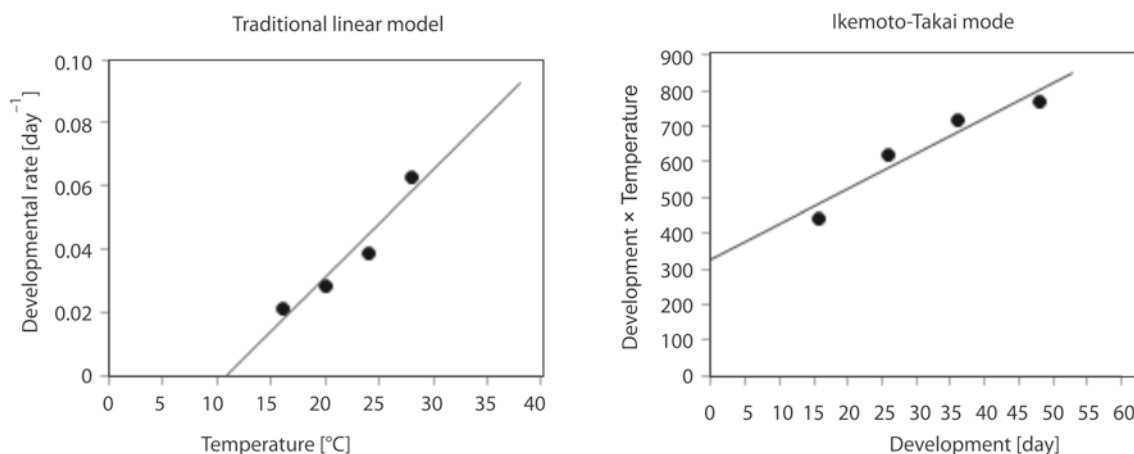The paired bootstrap test showed that increasing the temperature from 16 to 32°C was significantly effective

Fig. 1. Fitting the linear models (line) to observed developmental rates (•) of overall immature stages of *Adalia decempunctata*
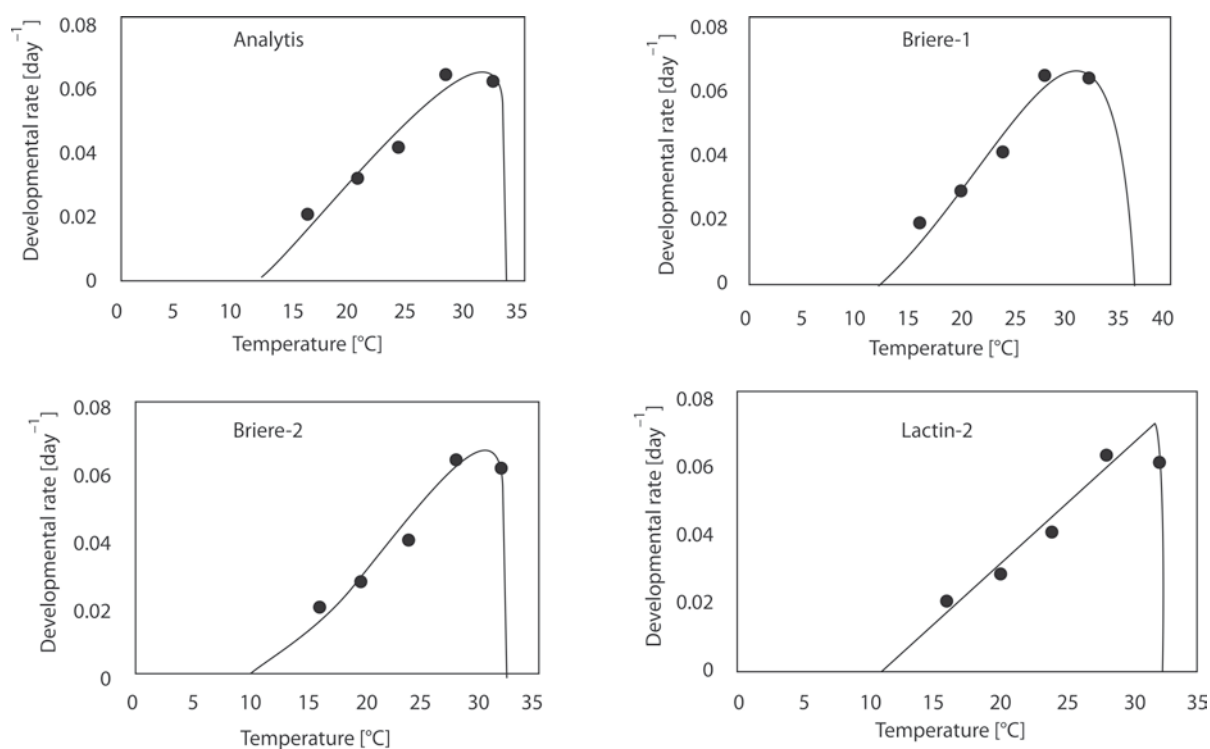

Fig. 2. Fitting the nonlinear model to observed developmental rates of *Adalia decempunctata* (•) observed data

on the longevity of female and male *A. decempunctata* fed *A. gossypii* ($p < 0.05$, Table 4). According to the results, temperature had a significant impact on oviposition including APOP (adult pre-oviposition period), TPOP (total pre-oviposition period), oviposition period and fecundity (Table 4). The mean of APOP was higher at 16°C with 8.76 ± 0.20 days, which decreased with the temperature increment. The mean TPOP of the reared ladybeetles indicated a significant decrease by elevating the temperature from 16 to 28°C which again increased significantly at 32°C (Table 4). The data presented in Table 4 showed that there was no significant difference between the mean of oviposition period at 16, 20 and 24°C ($p > 0.05$). However, the oviposition period of females significantly diminished by

augmenting the temperature from 28 to 32°C. Furthermore, the results revealed that temperature was effective on the oviposition of *A. decempunctata* ($p < 0.05$, Table 4), and the highest amount of fecundity occurred at 24°C (2469.58 ± 69.84 offspring/female).

Figure 3 displays the age-stage-specific survival rate (s_{xj}) of the ladybeetles fed *A. gossypii* at five constant temperatures, demonstrating the survival possibility of a newly laid egg into age x and stage j. These survival curves and differences between the stages represent the overlap in stages and changes in developmental rates among individuals (Chi and Su 2006). This study revealed that the highest and lowest survival rates were observed at 16 and 32°C in both males and females.

Table 3. Estimated parameters and goodness of fit of the nonlinear models fitting to developmental rates of *Adalia decempunctata*

Model	Parameters	Egg	Larvae	Pupa	Immature
Analytis	a	0.0384498202	0.0068661183	0.0098148911	0.0030041185
	T_{min}	12.98	12.39	12.20	11.99
	T_{max}	32.30	32.30	32.81	33.14
	n	0.8642232397	0.0952022227	1.1543599323	1.0093538721
	m	0.0773116522	0.0469919028	0.1105814712	0.0934127279
	T_{fast}	30.8	31.5	31.1	31.5
	R^2_{adj}	0.9480	0.8775	0.9146	0.8963
	AIC	−33.25	−42.71	−.34.08	−49.44
Briere -1	a	0.0003762456	0.0000722169	0.0001720785	0.0000452881
	T_{min}	12.02	11.79	10.16	12.24
	T_{max}	35.38	37.53	38.58	36.65
	T_{fast}	29.9	31.7	32.2	31.1
	R^2_{adj}	0.9583	0.8767	0.911	0.9036
	ACI	−34.38	−42.73	−33.88	−49.873
Briere -2	a	0.000502238	0.0001873641	0.0004978704	0.0000930128
	d	2.9754477631	7.5284182043	6.8979068529	5.5818262521
	T_{min}	10.21	11.096	10.74	10.30
	T_{max}	34.02	32.33	32.43	32.75
	T_{fast}	30	30.8	30.8	30.7
	R^2_{adj}	0.9686	0.9140	0.9467	0.9310
	AIC	−35.79	−44.54	−36.43	−51.488
Lactin -2	P	0.0178742632	0.005381709	0.0134491352	0.0032390898
	ΔT	0.7180643911	0.1305454126	0.0556434777	0.1371999796
	λ	−1.187868563	−1.060167652	−1.164272748	−1.035765075
	T_{max}	33.84	32.53	32.16	32.61
	T_{min}	9.7	11.8	11.40	10.8
	T_{fast}	30.8	31.7	31.9	31.7
	R^2_{adj}	0.9759	0.9049	0.9432	0.9277
	AIC	−37.11	−44.03	−36.12	−51.25

T_{min} – the lower temperature threshold; T_{max} – the upper temperature threshold; T_{fast} – the fastest developmental temperature; R^2_{adj} – adjusted coefficients of determination; AIC – the Akaike information criterion to appraise goodness of fit of nonlinear models; a, n, m, d, λ, P and ΔT – the constant coefficients for the model's suitability

Table 4. Longevity of adults and reproductive characteristics of *Adalia decempunctata* females reared on *Aphis gossypii* at five constant temperatures

Statistics	No	16°C	No	20°C	No	24°C	No	28°C	No	32°C
TPOP [d]	17	60.24 ± 0.77 a	20	43.45 ± 0.72 b	32	29.33 ± 0.46 c	33	18.12 ± 0.4 e	21	21.67 ± 0.63 d
APOP [d]	17	8.76 ± 0.20 a	20	5.15 ± 0.15 b	32	2.58 ± 0.10 c	33	2.61 ± 0.11 c	21	2.52 ± 0.15 c
O_d [d]	17	81.35 ± 3.56 a	20	81.50 ± 2.35 a	32	85.58 ± 1.76 a	33	65.15 ± 1.74 b	21	51.43 ± 1.35 c
F (all females)	17	1,099 ± 68.58 d	20	1,441.25 ± 51.60 c	32	2,469.58 ± 69.84 a	33	1,680.79 ± 48.94 b	21	1,135.62 ± 32.4 d
Adult longevity [d]	39	111.74 ± 2.15 a	44	101.73 ± 2.44 b	53	95.98 ± 0.89 c	69	82.78 ± 1.44 d	44	69.98 ± 1.72 e
Female longevity [d]	17	110.00 ± 3.69 a	20	101.15 ± 3.34 ab	33	96.28 ± 1.24 b	33	85.00 ± 1.66 c	21	64.81 ± 1.93 d
Male longevity [d]	22	113.09 ± 2.58 a	24	102.21 ± 3.57 b	20	95.60 ± 1.23 b	36	80.75 ± 2.28 c	23	74.70 ± 2.43 c

No – sample size. Mean values in each row followed by the same letter are not significantly different (paired bootstrap test at 5% level); TPOP – total pre-oviposition period; APOP – adult pre-oviposition period; O_d – oviposition days; F – fecundity; d – days
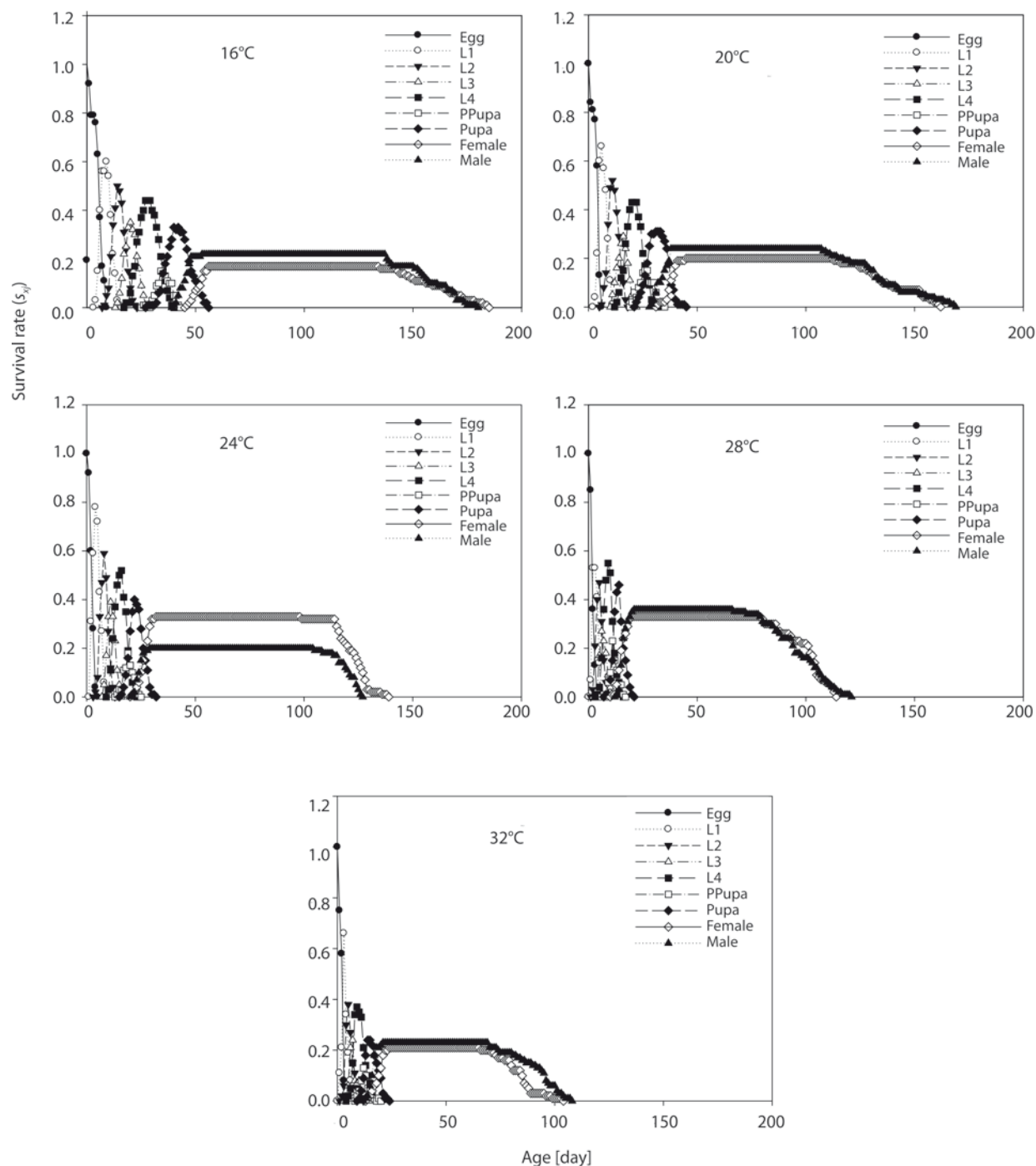
Fig. 3. Age-stage specific survival rate (s_{xj}) of *Adalia decempunctata* at five constant temperatures. L1–L4 – instar larvae, PPupa – prepupa

The age-specific survival rate (l_x), age-specific fecundity (m_x), and age-specific maternity ($l_x\,m_x$) of *A. decempunctata* at five constant temperatures are demonstrated in Figure 4. The l_x curve indicates that the ladybeetles reared on *A. gossypii* could be alive for 184 days at 16°C and 107 days at 32°C (Fig. 4). The m_x and $l_x m_x$ curves reveal a higher fecundity rate of this predator fed *A. gossypii* at 24 and 28°C. The highest major peak of the daily fecundity of females occurred on days 48 and 34 at 24 and 28°C, respectively (Fig. 4).

The life expectancy (e_{xj}) is the expected time that one individual will live from age x to stage j. The e_{xj} of female ladybeetles ranged from 69.95 to 115.47 days at different temperatures. Since this study was done under laboratory conditions without the negative effects of field conditions, the life expectancy gradually decreased with aging (Fig. 5).

The parameter V_{xj} is the contribution of individuals at age x and stage j to the future population. Our results confirmed that females had the greatest contribution to
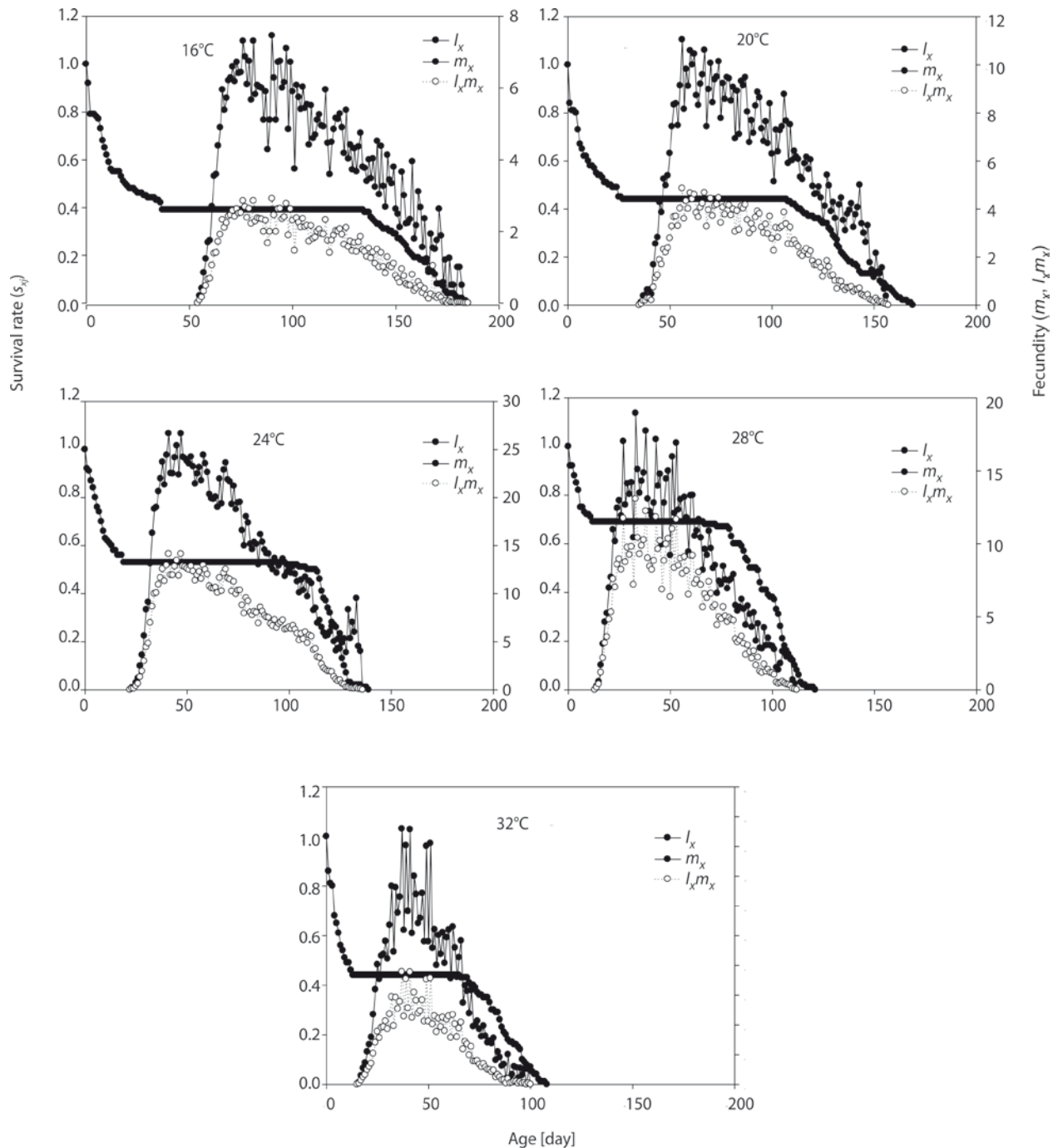
Fig. 4. Age-specific survival rate (l_x), age-specific fecundity (m_x) and age-specific maternity ($l_x m_x$) of *Adalia decempunctata* at five constant temperatures

the population of ladybeetles at the ages of 69, 56, 40, 33 and 37 days at 16, 20, 24, 28 and 32°C, respectively. The reproductive rate increased significantly with the start of reproduction (Fig. 6).

Population growth parameters

Table 5 presents the population growth parameters of *A. decempunctata* at five constant temperatures. The paired bootstrap test demonstrated that the highest value of r was (0.1945 d^{-1}) at 28°C and the lowest (0.0592 d^{-1}) at 16°C (Table 5). The recorded λ values were also similar to r, which varied from 1.0610 d^{-1} at 16°C to 1.2148 d^{-1} at 28°C. According to the recorded data, the longest and shortest T was 88.23 ± 0.94 days at 16°C and 32.47 ± 0.54 days at 28°C. The R_0 at 24°C (814.96 ± 119.09 offspring) and 28°C (554.66 ± 79.82 offspring) was the highest compared to other temperatures (Table 5).
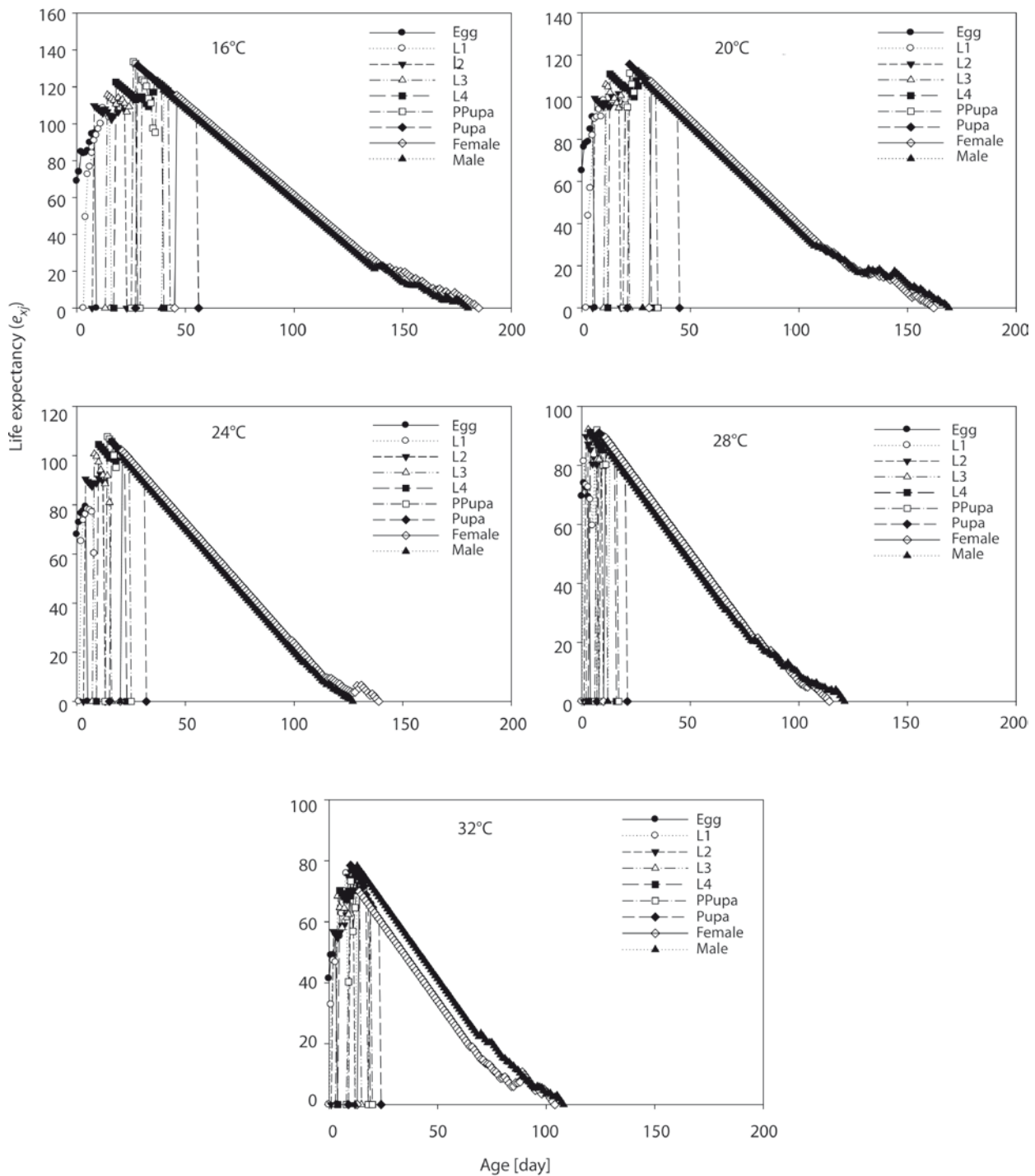
Fig. 5. Age-stage-specific life expectancy (e_{xj}) of *Adalia decempunctata* at five constant temperatures. L1–L4 – instar larvae, PPupa – prepupa

Table 5. Life table parameters (means ± SE) of *Adalia decempunctata* reared at five constant temperatures

Population parameters	16°C	20°C	24°C	28°C	32°C
r [d^{-1}]	0.0592 ± 0.0031 d	0.0831 ± 0.0037 c	0.1413 ± 0.0041 b	0.1945 ± 0.0066 a	0.1486 ± 0.0074 b
λ [d^{-1}]	1.0610 ± 0.0033 d	1.0867 ± 0.004 c	1.1518 ± 0.0048 b	1.2148 ± 0.0080 a	1.1602 ± 0.0086 b
R_0 (offspring)	186.83 ± 42.97 b	288.25 ± 58.19 b	814.96 ± 119.09 a	554.66 ± 79.82 a	238.48 ± 46.82 b
T [d]	88.23 ± 0.94 a	68.11 ± 1.03 b	47.40 ± 0.627 c	32.47 ± 0.54 e	36.82 ± 0.92 d

Mean values in each row followed by the same letter are not significantly different (paired bootstrap test at 5% level); r – intrinsinc rate; λ – finite rate of increase; R_0 – net reproductive rate; T – mean generation time
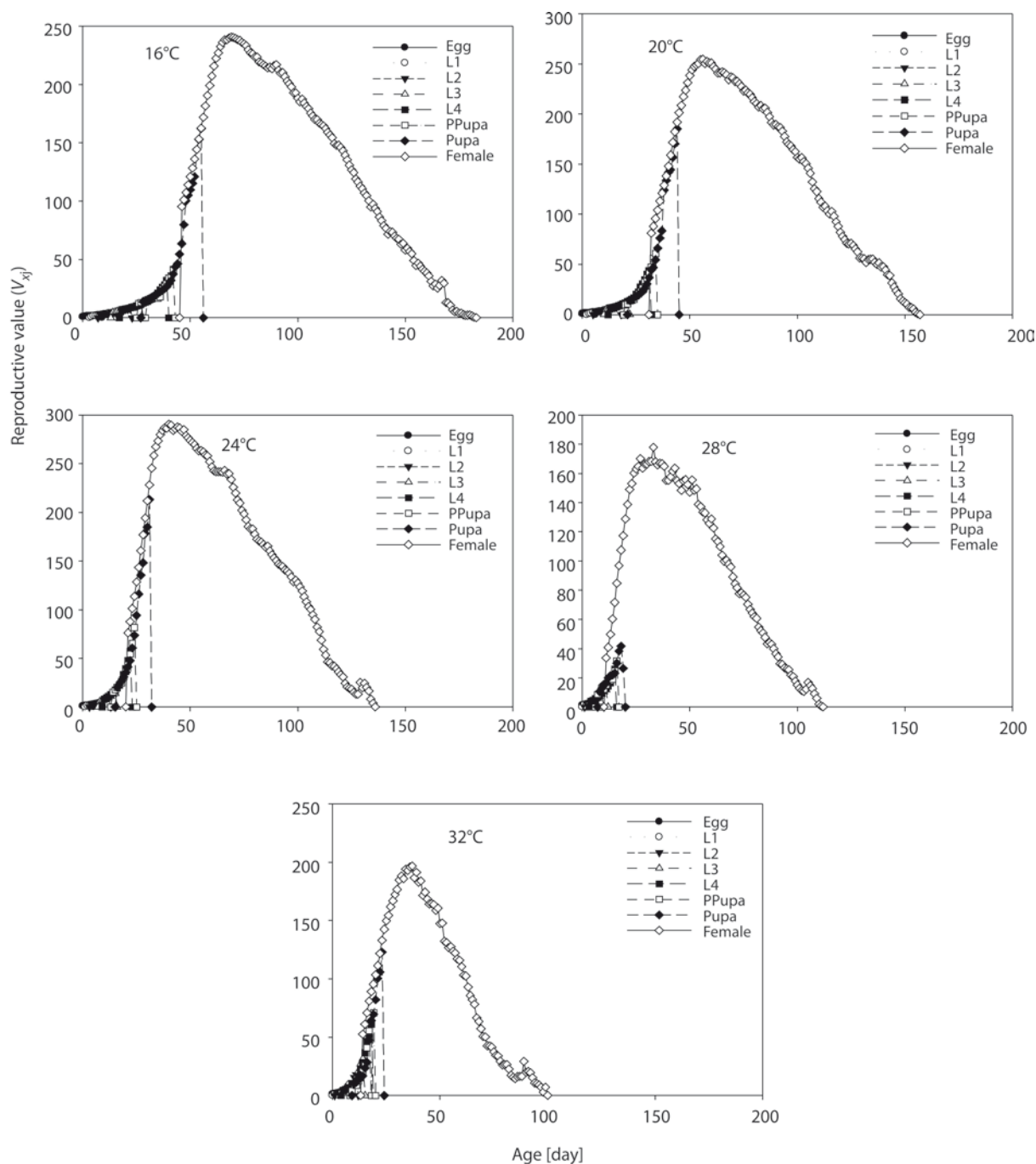
Fig. 6. Age-stage-specific reproductive value (V_{xj}) of *Adalia decempunctata* at five constant temperatures. L1–L4 – instar larvae, PPupa – prepupa

Discussion

Our results clearly revealed that the developmental time, survival, and fecundity of *A. decempunctata* is influenced by various temperatures. The successful developmental cycle was observed from 16 to 32°C. In this temperature range, the developmental time was inversely reduced by increases in temperature from 16 to 28°C and then increasing at 32°C. A similar trend has also been reported by other researchers in their respective studies on coccinellids (Katsarou

et al. 2005; Atlihan and Chi 2008; Jalali *et al.* 2009; Jalali *et al.* 2010; Satar and Uygun 2012). The shorter pre-adult developmental time at the higher temperatures can be explained by increased enzymatic activities and metabolism facilitating growth of insects (Atlihan and Chi 2008). The results of the current study showed that the overall survival rate of immature stages increased from 39% at 16% to 69% at 28°C, but diminished at 32°C. Eggs and first instar larvae had the highest mortality at 16 and 32°C. These results were similar to those of Skouras and Stathas (2015) who found that

the highest mortality rate of *Hippodamia* variegata (Goeze) was in eggs and first instar larvae.

Linear models are commonly used to estimate T_{min} and K values (Karimi-Malati *et al.* 2014). Our results showed that the developmental rate of *A. decempunctata* had a positive relationship with temperatures from 16 to 28°C and then a negative relationship at 32°C. To the best of our knowledge, no research has been conducted on the developmental rate of *A. decempunctata* based on linear models. There is only one study by Hodek (1973) who reported 9.1°C and 390 *DD* for the developmental threshold and thermal constant of *A. decempunctata*, respectively which were different from our findings using a traditional linear model. The differences could be due to the type of prey species, food quality, and laboratory conditions as well as genetic differences and geographic origin (Lee and Roh 2010; Skouras and Stathas 2015). The lower temperature threshold and thermal constant were respectively reported for *Harmonia axyridis* (Pallas) of 11.2°C and 231.3 *DD* (Schanderl *et al.* 1985), 11.2°C and 267.3 *DD* (Lamana and Miller 1998), 11.2°C and 258.2 *DD* fed on *Aphis fabae* and 10.8°C and 243.6 *DD* fed on *Dysaphis crataegi* (Stathas *et al.* 2011), for *Hippodamia convergens* (Guerin-Meneville) of 12.6°C and 228 *DD* (Miller 1992), for *Coccinella septempunctata* of 10.7°C and 281.5 *DD* (Katsarou *et al.* 2005) for *Adalia bipunctata* L. 10.06°C and 267.90 *DD* (Jalali *et al.* 2010) and for *Chilocorus bipustulatus* L. 12.4°C and 474.7 *DD* (Eliopoulos *et al.* 2010).

Some nonlinear models are used to determine critical temperatures, higher and lower temperature thresholds and the fastest developmental temperature (Analytis 1981; Schoolfield *et al.* 1981; Lactin *et al.* 1995; Briere *et al.* 1999). In this study, four nonlinear models including Analytis, Briere-1, Briere-2 and Lactin-2 were used to describe the developmental rate versus the temperature curve, since the relationship between temperature and developmental rate at very high and low temperatures was curvilinear. Accordingly, high R^2_{adj} values (0.9759 and 0.8767) for all the nonlinear models showed that the models adequately described our data. High R^2_{adj} values are not the only factors sufficient to select the most proper model for the observed data. However, a common method for evaluating the accuracy of critical temperature estimates is to compare them with experimental data (Kontodimas *et al.* 2004). T_{fast} value was estimated as 31.5, 31.1, 30.7 and 31.7°C using nonlinear models of Analytics, Briere-1, Briere-2 and Lactin-2, respectively. However, the lowest developmental period was observed at 28°C in the laboratory for all stages. Several researchers believe that the temperature at which the developmental time is the lowest can be considered as the optimal temperature (Aghdam *et al.* 2009; Zahiri *et al.* 2010). T_{fast} is the

temperature at which the developmental rate reaches its maximum, and where high mortality might also occur. On the other hand, at an optimal tempreture, the population size might be maximal with a low mortality (Shi *et al.* 2013). T_{max} value was satisfactorily estimated at 33.14, 32.75, and 32.61°C using Analytis, Briere-2 and Lactin-2 models, respectively, since in this study the eggs were unable to develop at 36°C. Among the utilized models, Briere-1 estimated 36.65°C for the overall immature stages which was slightly higher than the observed experimental data.

We demonstrated that female fecundity traits of *A. decempunctata* were also affected by temperatures. The longest and shortest TPOP values were recorded at 16 and 28°C due to the developmental time of immature stages. In contrast, APOP of female insects was longer at 16°C. Our results were similar to those of Satar and Uygun (2012), who reported the longest APOP at 15°C for *Scymnus subvillosus* (Goeze). Our findings revealed that temperature was also effective on the adult longevity. The adults (males and females) had the longest longevity of 111.74 days at 16°C and the shortest longevity of 69.98 days at 32°C. *A. bipunctata* (Jalali *et al.* 2009) and *S. subvillosus* (Atlihan and Chi 2008) also showed similar results at different temperatures. In these two species, male and female longevities also decreased with higher temperatures. According to the results of the present study, the fecundity rate of *A. decempunctata* was the highest at 24 and 28°C and the lowest at 16°C. Our results were close to the findings reported by Satar and Uygun (2012). The females of *S. subvillosus* had different fecundity rates at 20, 25, 30 and 35°C, where the lowest and the highest fecundity rates were observed at 20 and 30°C.

A comparison of life table parameters of *A. decempunctata* fed *A. gossypii* at different temperatures (16 to 32°C) indicated that temperature had a significant effect on the biological parameters. The obtained data confirmed that the highest r and λ values were observed at 28°C and led to a better population growth of the predator. In contrast, these parameters remarkably decreased at 16°C due to the high mortality rate and lower fecundity. Atlihan and Chi (2008) showed a similar effect of temperature on the intrinsic rate of increase (r) and the finite rate of increase (λ) in *S. subvilosus*. Both of the aforesaid parameters in their studies increased from 20 to 30°C and were related to shorter preadult developmental time, a higher daily rate of progeny production and an earlier peak of reproduction, which dropped suddenly at 35°C indicating increased immature mortality and reduced fecundity rate.

Chi (1988) showed the relationship between the mean fecundity (F) and R_0 as $R_0 = F \times (N_f/N)$, where: N – the total number of eggs used for the life table study

at the beginning and N_f – the number of emerged female adults). All of our values for F and R_0 of *A. decempunctata* were consistent with the results given by Chi (1988). Although the highest fecundity and R_0 were recorded at 24°C, a lower survival rate (53%) and longer total developmental time (25.96 days) led to a lower r value at 24°C compared with 28°C. It seems that the changes in the developmental rates and survival rates affected the r value more significantly than the variations in oviposition rates and fecundity. Huey and Berrigan (2001) found that although shorter developmental time and higher fecundity led to higher r values, developmental time was a much stronger predictor of r than fecundity. The mean generation time (T) of *A. decempunctata* was also affected by temperature, where the shortest T value was observed at 28°C with a resulting r value that was the highest at this temperature. The T is inversely related to temperature and r is inversely related to generation time in ectotherms, whereas R_0 is independent of T. Consequently, the shortening of T at high temperatures (in a normal range) will increase r but will not affect R_0 (Huey and Berrigan 2001).

The results of characterizing the effect of different temperatures on developmental stages of *A. decempunctata* suggest that developmental time decreased with temperature rise. It should be considered that choosing the best temperature based on reducing the developmental period is not suitable because of high mortality. It seems that utilizing the effect of temperature on the mortality process as well as life table parameters would be more reasonable and accurate for selecting the appropriate temperature (Ramzani and Samih 2016). Amarasekare and Savage (2012) also believe that the temperature, at which the r value is the highest, should be chosen as the proper temperature. Accordingly, and based on the results of the current study, 28°C was chosen as the proper temperature due to lower growth and developmental period, high survival rate, and higher r and λ, compared to other examined temperatures. Since in natural environments most of the populations are affected by various biotic and abiotic factors (Atlihan and Chi 2008), the results based on laboratory studies should be used cautiously (Agarwala *et al.* 2003). For practical application and benefit of *A. decempunctata* as a biological agent, more studies are needed on the development of both prey and predator populations to achieve a desirable outcome. The suitability of *Ephestia kuehniella* Zeller eggs and *A. gossypii* as two appropriate hosts for *A. decempunctata* has already been reported (Mojib-Haghghadam *et al.* 2018). Thus, both the earlier and current results can provide basic and useful data in studying population dynamics, mass rearing programs, and aphid management in the future.

Conclusions

The linear and nonlinear models used in the present study on biological and population growth parameters of *A. decempunctata* clearly showed that this species is a useful biological control agent against aphids. This usefulness could be of particular importance in areas with a mild climate and a temperature range of 16 to 32°C. The study could also provide useful information for designing mass rearing by setting the appropriate temperature for the maximal survival and population development. Determining critical temperatures is useful to understand the distribution potential and abundance of predator populations (Messenger 1970). For this predator to be more effective in biological control programs, the temperature requirements of the ladybeetles hosts should be identified and adapted to the growth requirements of the predator in order to make appropriate decisions in integrated pest management.

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