

Article

Demographic characteristics of *Bryobia rubrioculus* (Acari: Tetranychidae) reared on sour cherry leaves at different constant temperatures

Mohammad Ali Soleimani*, Mohammad Khanjani, Babak Zahiri and Saeid Javadi Khederi

Department of Plant Protection, Faculty of Agriculture, Bu-Ali Sina University, Hamedan, Iran; E-mails: soleimani.m.a@gmail.com, mkhanjani@gmail.com, bzahiri@basu.ac.ir, Javadis84@gmail.com

*Corresponding author

Abstract

The life history of *Bryobia rubrioculus* Scheuten (Acari: Tetranychidae) on sour cherry leaves was studied based on the age-stage, two-sex life table at nine constant temperatures (15, 17.5, 20, 22.5, 25, 27.5, 30, 32.5 and 33.5 °C), 60 ± 5% RH and a photoperiod of 16: 8 (L: D) h. The longest and shortest total development time of the mites were obtained as 62.6 ± 1.66 and 14.2 ± 0.20 days at 15 and 32.5 °C, respectively. As temperature increased from 15 to 32.5 °C, the life span of the mites decreased from 83.5 ± 2.14 to 24.7 ± 0.39 days, respectively. The highest and lowest total fecundity was observed as 37.3 ± 1.63 and 6.3 ± 1.06 eggs at 17.5 and 15 °C, respectively. The highest intrinsic rate of increase (r) was obtained as 0.1108 ± 0.005 d⁻¹ at 30 °C. The mean generation time (T) ranged from 78.1 ± 2.8 to 19.1 ± 0.2 days at 15 and 32.5 °C. Survivorship data (l_x) of adult females were summarized and compared using the shape and scale parameters of the Weibull frequency distribution model. The lower temperature threshold (t) and thermal constant (k) of the immature stages were estimated using the Ikemoto and Takai's linear model to be 8.9 °C and 361.3 degree days (DD), respectively. The optimum temperatures were calculated by selected non-linear models including Analytis1/Allahyari, Hilbert and Logan, and Logan-6 models to be 33.10, 33.90 and 32.40 °C, respectively.

Key words: developmental time; life table; Prostigmata; temperature; thermal constant.

Introduction

Most polyphagous mites associated to sour cherry throughout the world are belonging to the family Tetranychidae (Khanjani and Haddad Iraninejad 2009). Among them, the brown mite, *Bryobia rubrioculus* Scheuten (Acari: Tetranychidae) has been considered as a major pest of sour cherry in many countries around the world, causing serious damage in many fruit trees such as plum, black cherry, sweet cherry and sour cherry in America, Europe and Asia, including western Iran (Meyer 1974; Jeppson *et al.* 1975; Khanjani and Haddad Iraninejad 2009). The feeding damage inflicted by the brown mite appears as whitish-grey spots on the upper surface of young or spur leaves (Jeppson

et al. 1975; Osakabe *et al.* 2000). Heavily infested plants become pale and may prematurely drop their leaves (Meyer 1987).

Population growth rates largely determine the pest status of spider mites (Janssen and Sabelis 1992). Climatic factors such as humidity, precipitation and especially temperature as well as plant genotype strongly effect the survival rate, reproduction, population growth rate, developmental time and other major life processes of poikilothermic arthropods (Sabelis 1985a; Roy *et al.* 2003; Mori *et al.* 2005; Gotoh *et al.* 2010). In addition, understanding the influence of climatic factors on the relevant life table parameters can be used for predicting population dynamics and efficacy of the subsequent management programs (Logan *et al.* 1976; Price 1997; Martin 2000; Demirel and Cabuk 2008). Demographic analysis has been widely applied to *B. rubrioculus* to quantify the intrinsic potential for population growth using life tables (Herbert 1962; Keshavarz Jamshidian 2004; Kasap 2008; Honarparvar *et al.* 2012; Javadi Khederi and Khanjani 2014; Javadi Khederi *et al.* 2014). By using life tables, the population growth parameters of a pest species can be detected (Sakai *et al.* 2001), and then the proper timing for pest control is possible (Chi 1990). Intrinsic potential for population growth is estimated using demographic analysis of life tables (Chi and Liu 1985; Chi 1988). The intrinsic rate of increase (r) combines the wide range of life table parameters *i.e.*, pre-imaginal survival, developmental rate, longevity of females, fecundity schedule and sex ratio into a single parameter and allows a direct assessment of the potential for pest population growth that is especially important for integrated pest management (Sabelis 1985b).

Temperature driven rate models have been frequently used to predict the occurrence and seasonal population dynamics of pests (Tobin *et al.* 2001) and to model trophic interactions in various ecosystems associated with possible consequences of global warming (Logan *et al.* 2006). Models enable us to describe the reproductive capacity and survival curve and to compare data with similar average values, which differ in their temporal distribution (Kontodimas *et al.* 2007). A variety of models as functions of temperature have been proposed to describe the relationship between temperature and arthropod development (Ludwig 1928; Janisch 1932; Davidson 1942; Pradhan 1945; Stinner *et al.* 1974; Logan *et al.* 1976; Sharpe and DeMichele 1977; Lactin *et al.* 1995; Briere *et al.* 1999; Ikemoto and Takai 2000). They vary with respect to parameter number and basic assumptions about temperature effects near lower and upper limits (Roy *et al.* 2002). Accumulation of degree-days to estimate events in pest development is a common approach to time sampling and management. Those predictions are all based on a linear relationship between temperature and development rate, which has been based on the thermal characteristic.

In this survey, we used linear and non-linear temperature-driven rate models that have been already proposed and are most commonly used to determine key bioclimatic parameters of arthropods. In addition, effect of constant temperatures on biological and demographic parameters were studied based on the age-stage, two-sex life table method. Therefore, the data obtained from this study can be used to compare the population growth potential of *B. rubrioculus* under various constant temperatures and forecast their potential abundance.

Materials and methods

Mite population source

The initial population of *B. rubrioculus* was collected from sour cherry orchards situated in Hamedan, western Iran (34° 48' N, 48° 28' E, 1830 m a.s.l.) in June 2010. The

stock culture was maintained on sour cherry leaf discs in a rearing chamber (25 ± 2 °C, $65 \pm 10\%$ RH, and photoperiod 16:8 (L: D) h. This culture was the source of all mites used in this study. Mites were reared for at least three consecutive generations prior to the experiments.

Development and biology of B. rubrioculus at different temperatures

Experiments were conducted on sour cherry leaf discs (*Prunus cerasus* L.) at 15, 17.5, 20, 22.5, 25, 27.5, 30, 32.5 and 33.5 ± 1 °C, $65 \pm 10\%$ RH, and a photoperiod 16:8 (L:D) h. In a preliminary incubation study in which temperatures were differing by 2.5 °C, eggs failed to hatch at 35 °C. Therefore, it was decided to determine more precisely the highest temperature at which eggs would hatch, by using 1 °C. Mature, but non-senescent sour cherry leaf discs were used as experimental areas. Each area consisted of a leaf placed on a layer of filter paper over a polystyrene pad saturated with distilled water in a 12 cm diameter Petri dish. Each leaf was covered with filter paper as a barrier to prevent the mites from escaping that had a 40 mm diameter opening in the center. Water was added daily to keep the filter paper and polystyrene pad moist, and to cover the base of the Petri dish. All leaves were placed upside-down. Leaf discs were renewed weekly. Approximately 25 adult females from the stock culture were introduced onto each leaf disc and allowed to lay eggs for a 12-h period. Eggs were transferred one at a time to a fresh leaf disc, as described above for rearing. The duration of each immature stages *i.e.*, egg incubation, larva, protochrysalis, protonymph, deutochrysalis, deutonymph and teliochrysalis, oviposition period, longevity and fecundity, were recorded daily (*i.e.*, every 24h). Assays were replicated 120 times and each leaf disc represented a replicate.

Statistical analysis

The development rate values (1/development time) were modeled as linear and non-linear functions of temperature. The ordinary regression method were not found to be the best for the modeling development rate of immature stages and also this method give us more reliable of parameters, so we used the Ikemoto and Takai's method. The Ikemoto and Takai's regression method (equation 1) expressed based on the law of "total effective temperature" (equation 2) was used as a linear model to estimate the respective parameters, where D indicates the duration of development; t , the lower temperature threshold and k , the effective cumulative temperature. (*i.e.*, thermal constant or number of day-degrees above the t necessary for the completion of a specific developmental stage). However, some of the data points at both ends of temperatures range need to be excluded to achieve satisfactory fitting within the intermediate temperature range in which the relationship is about linear (Ikemoto and Takai 2000).

$$DT = k + tD \quad (1)$$

$$D(T - t) = k \quad (2)$$

Development rate values were also modeled as a non-linear function of temperature using non-linear models (equations 3, 4 and 5, respectively) to estimate the respective parameters, where T_{\min} , T_{opt} , and T_{\max} indicates the bioclimatic parameters.

$$\text{Analytis 1/Allahyari (3) (Allahyari 2005) } r(T) = P\delta^n (1 - \delta^m), \delta = (T - T_{\min}) / (T_{\max} - T_{\min})$$

$$\text{Logan-6 (4) (Logan et al. 1976) } r(T) = \psi [e^{\rho T} - e^{\rho(T_L - \tau)}], \tau = T_L - T / \Delta T$$

Hilbert and Logan (5) (Hilbert and Logan 1983) $r(T) = \psi \left[\frac{(T-T_b)^2}{(T-T_b)+D^2} \right] - e^{-[(T_m-(T-T_b))/\Delta T]}$

Estimates of the models parameters were accomplished using the non-linear platform of JMP version 8.0.2 (SAS Institute 2009). Sum of squares error (*SSE*) is the objective that is to be minimized during the iteration process. The best fit of the model was assessed and decided on by comparing the *SSE* of each iteration result. The bio-climatic parameters (*i.e.*, T_{\min} , T_{opt} , and T_{\max}) were either directly estimated by the fitted model or model performance evaluation was made based on both goodness-of-fit and biological significance. Also, the Akaike information criterion (AIC) (equation 6) were used to appraise goodness-of-fit of non-linear models (Akaike 1974). Where n is the number of observations, p is the number of model parameters and *SSE* is the sum of squares for the model error term. The model that has the smallest value of AIC is considered the best. Bioclimatic criteria were compared with observed data to assess their biological significance.

$$\text{AIC} = n \ln (SSE/n) + 2p \quad (6)$$

Because the age-specific survival rate should not be fitted to an equation while ignoring the closely related age-specific fecundity and its consequent effect on the population parameters, we suggest that the use of Weibull function model should be reconsidered (equation 7), where x is female age (day) and b and c are model parameters (Pinder *et al.* 1978). In the Weibull model, b is the scale parameter that is inversely related to the mortality rate, and c is the shape parameter that allows the model to produce survival distributions of different forms, from exponential to an extreme inverted S shape (Kontodimas *et al.* 2007).

$$l(x) = \text{Exp} (-[x/b]^c) \quad \text{Weibull (7)}$$

The life history raw data of all individuals were analyzed based on the age-stage, two sex life table method (Chi and Liu 1985; Chi 1988) by using the Two-sex-MS-Chart software (Chi 2014) designed by Hsin Chi. The age-specific survival rate (l_x), gross maternity (m_x), expectation of life (e_x) and demographic parameters including r , intrinsic rate of increase; R_0 , net reproductive rate and T , the mean generation time, were calculated accordingly (equations 8–12).

Intrinsic rate of increase was calculated by using the iterative method from the Euler-Lotka equation (equation 10) with age started from 0 (Goodman 1982).

$$R_0 = \sum_{x=0}^{\infty} l_x m_x \quad (8)$$

$$GRR = \sum m_x \quad (9)$$

$$\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1 \quad (10)$$

$$\lambda = e^r \quad (11)$$

$$T = \ln (R_0)/r \quad (12)$$

The mean generation time (T) is defined as the period of time that a population can increase to R_0 -fold of its size at the stable age-stage distribution. The life expectancy (e_{xy}),

i.e., the time that an individual of age x and stage y is expected to live, was calculated according to the method described by Chi and Su (2006) (equation 13), where m is the number of developmental stages and s'_{ij} is the probability that an individual of age x and stage y will survive to age i and stage j .

$$e_{xy} = \sum_{i=x}^n \sum_{j=y}^m s'_{ij} \quad (13)$$

The means and standard errors of the life table parameters were calculated by using the Bootstrap method (the Bootstraps repetitions were equal to 1000) (Huang and Chi 2012). The computer program Two-Sex-MS-Chart was used for Bootstrap estimation (Chi 2014). All graphs were produced by Sigma Plot (version 11.0) (Systat Software Inc. 2008).

Results

Pre-imaginal development

Developmental times of *B. rubrioculus* at nine constant temperatures are shown in Table 1. At the maximum temperature tested (34.5 °C) eggs failed to hatch, whereas they hatched and successfully developed to the adulthood stage from 15 to 33.5 °C (Table 1). Developmental time decreased as the temperature increased from 15 to 32.5 °C while overall this value increased from 32.5 to 33.5 °C. The shortest development time for all stages occurred at 32.5 °C. At 33.5 °C, only 30 eggs of 200 cohort individuals developed to adulthood, whereas at 34.5 °C, egg hatching was not observed, indicating that 34.5 °C is out of development temperature range and can be consider as lethal temperature. Immature longevity was the lowest at 15, 32.5, 33.5 °C and particularly its occurred during the larval stages (Fig. 4).

Modeling development rates

A positive relationship observed between development rate and temperature up to the upper limit of 32.5 °C, followed by an inverse relationship. Lower development threshold (t) and thermal constant (k) of each immature stage of brown mite was estimated using the Ikemoto and Takai's model within particular temperature ranges from 15 to 32.5 °C (Table 2). The lower development threshold for total immature development was estimated to be 8.9 °C and based on the threshold of development mites required 361.3 °C degrees-days for completion of their life cycle (egg to adult) (thermal constant) (k) (Table 2).

The non-linear models (equations 3–5) were selected based on goodness of fit by low AIC values and biological significance (Table 3). Three models, Analytis-1/Allahyari, Hilbert and Logan, and Logan-6 gave a good fit to the data for entire immature development (Fig. 1). Regarding these models, critical temperatures of entire immature stages were mathematically computed to be 7.0, 33.1, and 33.7 °C, respectively, using the Analytis-1/Allahyari model. In addition, the optimum and maximum temperature (T_{opt} and T_{max}) were calculated to be 32.8, 33.9 °C and 32.4, 34.2 °C for entire immature using Hilbert and Logan and Logan-6, respectively (Table 3).

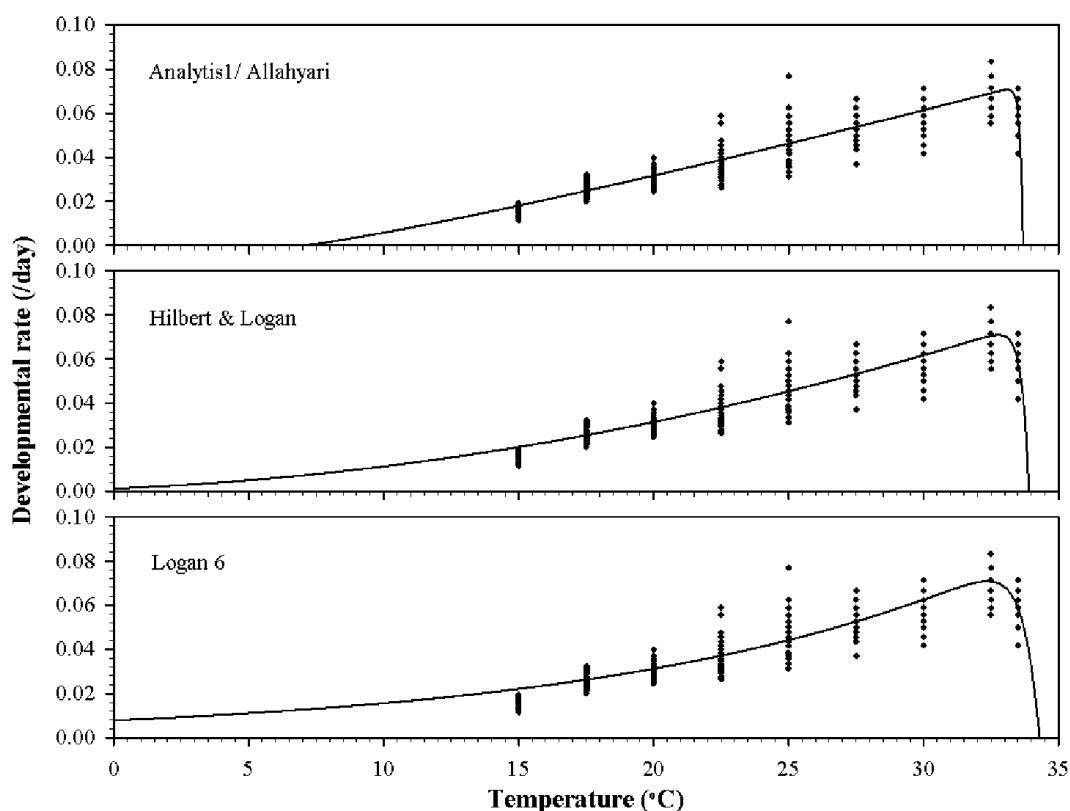


Figure 1. Observed (dots) and predicted (lines) development rate of entire immature stages of *Bryobia rubrioculus*. Predicted values are non-linear models estimates. Critical temperatures (T_{min} , T_{opt} , T_{max}) computed using non-linear platform of JMP software.

Table 1. Mean \pm SE duration (day) of immature stages of *Bryobia rubrioculus* at nine constant temperatures.

Temp. (°C)	Initial individuals	Egg	Larva	Proto-chrysalis	Proto-nymph	Deuto-chrysalis	Deuto-nymph	Telio-chrysalis	Total immature	
15	38	DT ^a	28.0 \pm 0.90	5.7 \pm 0.54	7.0 \pm 0.32	5.2 \pm 0.49	5.3 \pm 0.20	5.2 \pm 0.44	6.0 \pm 0.29	62.6 \pm 1.66
		R ^b	23-48	2-17	3-14	2-15	3-8	1-13	2-9	52-88
17.5	120	DT	21.2 \pm 0.21	1.5 \pm 0.06	4.3 \pm 0.10	1.9 \pm 0.09	3.8 \pm 0.09	2.1 \pm 0.07	4.6 \pm 0.07	38.7 \pm 0.33
		R	15-27	1-4	2-8	1-5	2-8	1-5	3-6	32-50
20	120	DT	17.3 \pm 0.26	1.3 \pm 0.05	3.3 \pm 0.08	1.8 \pm 0.08	3.0 \pm 0.06	2.0 \pm 0.07	3.7 \pm 0.08	32.6 \pm 0.33
		R	13-25	1-3	1-8	1-6	1-5	1-5	2-7	25-42
22.5	56	DT	13.4 \pm 0.48	1.4 \pm 0.08	2.7 \pm 0.12	1.7 \pm 0.12	2.7 \pm 0.16	1.6 \pm 0.08	3.1 \pm 0.07	26.9 \pm 0.58
		R	5-24	1-3	1-5	1-5	1-8	1-3	2-5	18-38
25	72	DT	9.7 \pm 0.26	1.3 \pm 0.09	2.0 \pm 0.09	1.8 \pm 0.08	2.0 \pm 0.11	1.9 \pm 0.10	2.5 \pm 0.09	21.5 \pm 0.40
		R	4-16	1-4	1-4	1-4	1-5	1-5	1-5	13-32
27.5	67	DT	8.9 \pm 0.14	1.4 \pm 0.09	1.9 \pm 0.12	1.4 \pm 0.09	1.5 \pm 0.10	1.5 \pm 0.08	1.9 \pm 0.08	18.9 \pm 0.30
		R	6-12	1-5	1-5	1-5	1-6	1-4	1-4	15-27
30	41	DT	8.9 \pm 0.11	1.3 \pm 0.08	1.6 \pm 0.18	1.2 \pm 0.09	1.4 \pm 0.09	1.3 \pm 0.08	1.5 \pm 0.10	17.5 \pm 0.30
		R	7-11	1-3	1-8	1-4	1-3	1-3	1-4	14-24
32.5	54	DT	7.5 \pm 0.15	1.0 \pm 0.00	1.0 \pm 0.01	1.1 \pm 0.05	1.1 \pm 0.05	1.1 \pm 0.05	1.2 \pm 0.05	14.2 \pm 0.20
		R	6-10	1-1	1-2	1-3	1-3	1-2	1-2	12-18
33.5	30	DT	9.0 \pm 0.14	1.2 \pm 0.08	1.6 \pm 0.23	1.2 \pm 0.12	1.3 \pm 0.10	1.3 \pm 0.08	1.5 \pm 0.09	17.3 \pm 0.34
		R	7-11	1-3	1-8	1-4	1-3	1-2	1-2	14-24

^a DT, Mean development time \pm SE.

^b R, Range of development time (minimum-maximum).

Oviposition

The oviposition period was significantly longer at lower temperatures, ranging from 24.6 ± 0.99 days at 17.5°C to 5.9 ± 0.46 days at 33.5°C . The pre-oviposition period decreased from 7.4 ± 0.40 days at 15°C to 1.2 ± 0.12 day at 33.5°C (Table 4, Fig. 2). The reproduction was strongly decreased at 15 and 33.5°C (Table 4). The highest progeny production was recorded on day 42 (2.5 eggs per female per day) at 22.5°C (Fig. 2). The observed age-specific fecundity (m_x) fluctuated throughout the oviposition period. Generally, curves showed an initial rapid increase and were associated with more gradual downward while this pattern was different at 15 and 33.5°C (Fig. 2). The mites were most fecund at 17.5°C (37.4 eggs per female) (Table 4). However, the brown mite achieved its highest gross maternity (m_x) at 22.5°C (Fig. 2).

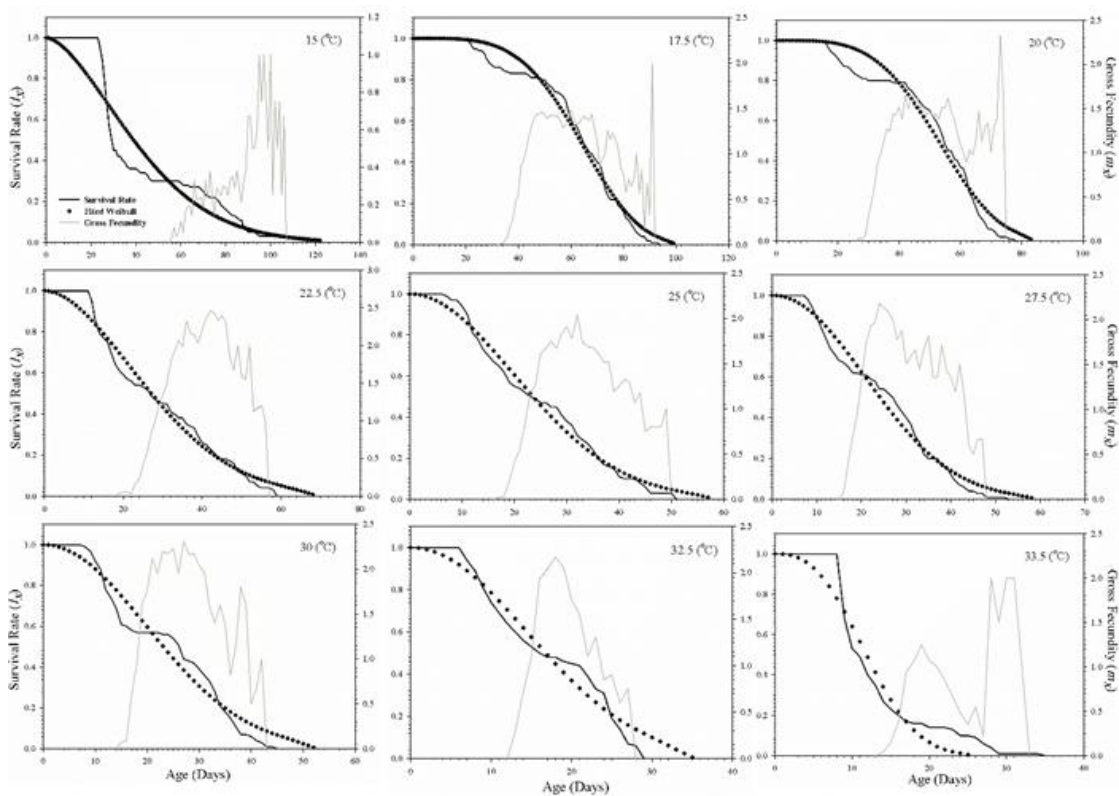


Figure 2. Weibull model fitted to the age-specific survival rate (l_x) and observed age-specific fecundity (m_x) of *Bryobia rubrioculus* at nine constant temperatures.

Adult longevity

With increasing temperature, *B. rubrioculus* longevity decreased (Fig. 2, Table 4). The highest longevity for adult females was obtained at 17.5°C (30.3 days) followed by that at 20.0°C (25.9 days) (Table 4). Age specific survivorship (l_x) data of adult females were fitted by Weibull frequency distribution at nine temperatures (Fig. 2). Maximum rate of mortality observed at 32.5°C , at which, surviving proportion (l_x) decreased more sharply than at 27.5 , 30 and 33.5°C (Fig. 2). The values of respective parameters obtained are presented in Table 5. Brown mites showed a greater rate of survival at lower temperatures than that at higher temperatures.

Table 2. Lower temperature threshold (t) and thermal constant (k) of the immature stages of *Bryobia rubrioculus* estimated by linear temperature-driven rate model (Ikemoto and Takai) at selected temperature ranges.

Developmental stage	Regression Linear		t (°C)	k (day-degree °C)
	Equation	r^2		
Egg	$y = 8.382x + 188.4$	0.909	8.3	188.4
Larva	$y = 11.646x + 18.67$	0.894	11.6	18.6
Protochrysalis	$y = 10.728x + 30.85$	0.960	10.7	30.8
Protonymph	$y = 10.051x + 23.70$	0.871	10.0	23.7
Deutochrysalis	$y = 9.931x + 29.49$	0.967	9.9	29.4
Deutonymph	$y = 9.665x + 25.39$	0.874	9.6	25.3
Teliochrysalis	$y = 10.150x + 34.06$	0.944	10.1	34.0
Immature	$y = 8.991x + 361.3$	0.959	8.9	361.3

Life expectancy and age-stage survival rates

The results showed that life expectancy (e_x) of newborn eggs increased from 45.37 days at 15 °C to 62.1 days (longest) at 17.5 °C and then decreased to 13.63 days at 33.5 °C (Fig. 3). The age-stage survival rates (s_{xj}) of brown mite at constant temperature are shown in Fig. 4. It shows the probability that an egg will survival to age x while in stage j . As the age-stage survival, takes the variable developmental rate among individuals stage, thus significant stage overlapping, could be observed.

Table 3. Selected non-linear temperature-driven rate models for describing developmental rate of entire immature stages of *Bryobia rubrioculus* based on statistical rank and biological.

Model	Model Parameter		Computed Points ^a	
	Parameter	Estimate±SE	Point	Value
Analytis-1/Allahyari	T_{min}	6.98 ± 2.09	T_{min}	6.9
	T_{max}	33.68 ± 23.09	T_{opt}	33.1
	n	1.16 ± 0.16	T_{max}	33.6
	m	243.14 ± 11.11		
	a	0.07 ± 0.07		
Hilbert and Logan	T_b	-4.88 ± 0.57	T_{opt}	32.8
	T_m	43.62 ± 13.04	T_{max}	33.9
	dT	0.26 ± 0.20		
	Y	7027557.33 ± 3.95		
	D	372417.65 ± 1.04		
Logan-6	T_m	34.29 ± 0.13	T_{opt}	32.4
	dT	0.57 ± 0.10	T_{max}	34.2
	Y	0.01 ± 0.00		
	p	0.07 ± 0.00		

^a Computed points were obtained mathematically using Advanced Grapher v2.11 and Graph Plotter v1.2 softwares

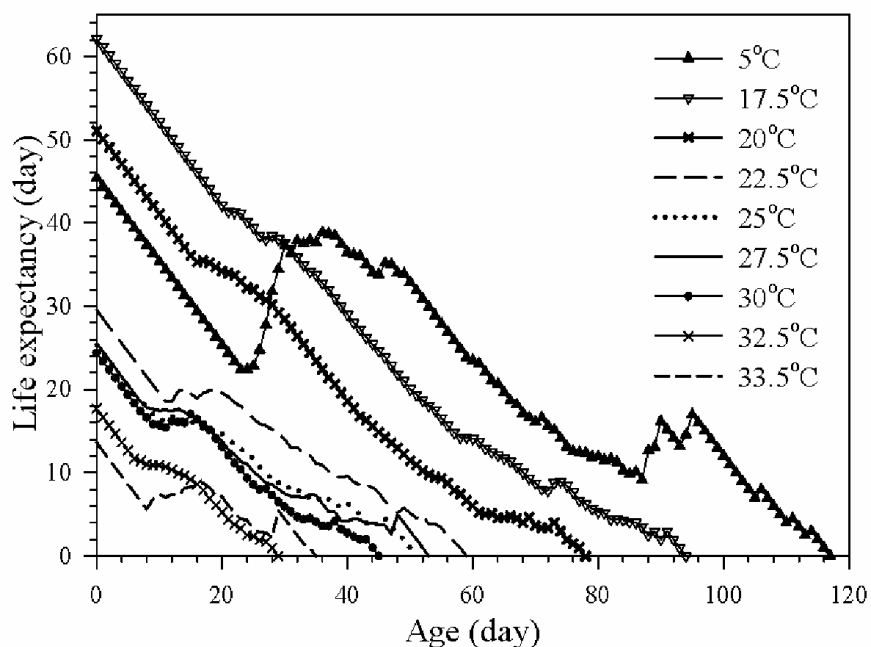
Stable population parameters

Demographic statistics indicated that the intrinsic rate of increase (r) increased from 0.0078 ± 0.005 to 0.1108 ± 0.003 day⁻¹ as temperature increased from 15 to 32.5 °C followed by a rapid fall at 33.5 °C. Mean generation time (T) decreased from 78.1 ± 2.8 to 19.1 ± 0.2 day as temperature increased from 15 to 32.5 °C (Table 6). Critical temperatures (T_{min} , T_{opt} and T_{max}) for intrinsic rate of increase parameters were about 15, 30 and 33.5 °C, respectively. The highest values of net and gross reproductive rate (R_0 and GRR) were observed at 17.5 °C (Table 6). Mites reared at 17.5 °C indicated a quick increase in net fecundity rate compared to mites reared at 15 °C; however, net fecundity decreased when they were reared at 33.5 °C. (Table 6).

Table 4. Life cycle statistics (days) and fecundity (eggs) of *Bryobia rubrioculus* at nine constant temperatures^a.

Temp. (°C)	Pre-imaginal period	Pre-oviposition period	Oviposition period	Post-oviposition period	Adult longevity	Life span	Total fecundity	Daily fecundity
15.0	62.6 ± 1.66	7.3 ± 0.40	8.6 ± 1.22	4.7 ± 0.44	20.8 ± 1.34	83.5 ± 2.14	6.3 ± 1.06	0.8 ± 0.05
17.5	38.7 ± 0.33	2.7 ± 0.13	24.6 ± 0.99	2.9 ± 0.19	30.3 ± 0.97	69.0 ± 1.06	37.3 ± 1.63	1.5 ± 0.03
20.0	32.6 ± 0.33	2.2 ± 0.06	20.6 ± 0.77	3.0 ± 0.16	25.8 ± 0.73	58.4 ± 0.81	36.1 ± 1.81	1.6 ± 0.04
22.5	26.9 ± 0.58	2.4 ± 0.15	11.4 ± 0.96	1.6 ± 0.13	15.5 ± 1.06	42.4 ± 1.20	28.7 ± 2.89	2.3 ± 0.13
25.0	21.5 ± 0.40	2.1 ± 0.13	9.7 ± 0.67	2.5 ± 0.19	14.4 ± 0.71	35.9 ± 0.86	23.1 ± 2.04	2.2 ± 0.08
27.5	18.9 ± 0.30	1.4 ± 0.07	11.3 ± 0.74	2.4 ± 0.20	15.2 ± 0.79	34.1 ± 0.84	26.8 ± 1.92	2.3 ± 0.08
30.0	17.5 ± 0.30	1.5 ± 0.10	12.0 ± 0.68	2.0 ± 0.19	15.6 ± 0.69	33.2 ± 0.81	28.6 ± 2.02	2.3 ± 0.10
32.5	14.2 ± 0.20	1.4 ± 0.12	6.2 ± 0.38	2.7 ± 0.21	10.5 ± 0.36	24.7 ± 0.39	15.7 ± 1.23	2.4 ± 0.11
33.5	17.3 ± 0.34	1.2 ± 0.14	5.8 ± 0.46	2.2 ± 0.24	9.3 ± 0.49	26.6 ± 0.60	8.4 ± 0.86	1.4 ± 0.08

^aThe values are given as Mean ± SE

**Figure 3.** Life expectancy (day) curves of *Bryobia rubrioculus* at nine constant temperatures.**Table 5.** Goodness of fit and parameters of Weibull model fitted to the age specific survivorship (l_x) of *Bryobia rubrioculus* at nine constant temperatures^a

Model	GF & P ^b	15.0°C	17.5°C	20.0°C	22.5°C	25.0°C	27.5°C	30.0°C	32.5°C	33.5°C
Weibull	SSE	1.04	0.20	0.31	0.12	0.07	0.11	0.20	0.11	0.21
	AIC	-553.87	-582.86	-432.70	-367.78	-337.65	-330.11	-246.53	-165.60	-182.03
	b	48.65	69.76	58.15	33.09	28.36	28.83	27.65	20.05	13.63
	c	1.64	4.09	3.84	1.83	1.97	2.06	2.03	2.05	2.61

^aThe values are given as mean.

^bGoodness of Fit (GF) and model Parameters (P); SSE is the Sum of Squares for Error and AIC is Akaike Information Criterion.

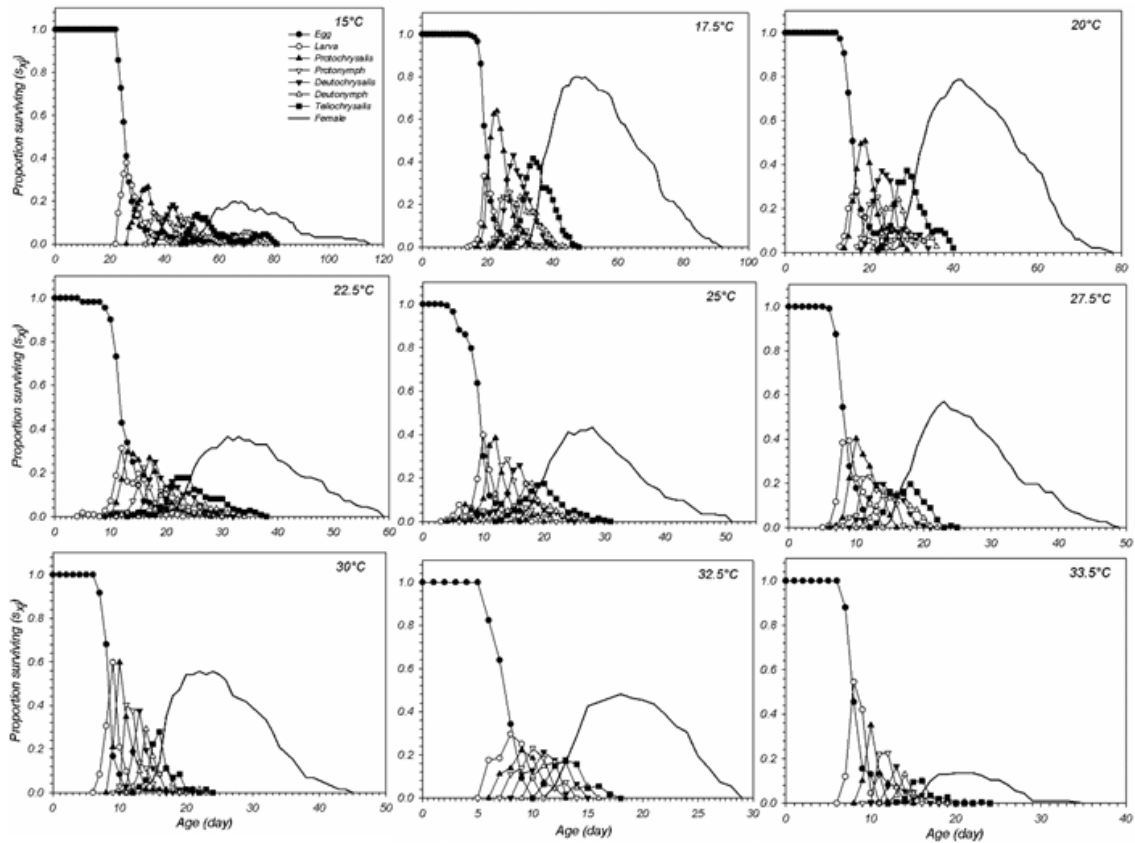


Figure 4. Age–stage specific survival rate (s_{xj}) of *Bryobia rubrioculus* at nine constant temperatures.

Table 6. Parameters related to potential rates of population increase of *Bryobia rubrioculus* obtained at nine constant temperatures^a.

Temp. (°C)	Intrinsic rate of increase (r)	Finite rate of increase (λ)	Gross reproductive rate (GRR)	Net reproductive rate (R_0)	Mean generation time (T)
15.0	0.0078 ± 0.0028	1.0078 ± 0.0028	18.8 ± 3.6	1.8 ± 0.3	78.1 ± 2.8
17.5	0.0644 ± 0.0010	1.0665 ± 0.0011	60.1 ± 2.8	31.1 ± 1.8	53.3 ± 0.4
20.0	0.0759 ± 0.0014	1.0789 ± 0.0015	58.4 ± 3.6	28.9 ± 1.8	44.2 ± 0.4
22.5	0.0737 ± 0.0039	1.0765 ± 0.0042	55.4 ± 3.4	14.3 ± 2.0	36.1 ± 0.7
25.0	0.0828 ± 0.0041	1.0863 ± 0.0045	39.9 ± 4.0	11.2 ± 1.3	29.2 ± 0.5
27.5	0.1060 ± 0.0044	1.1119 ± 0.0049	44.3 ± 3.2	15.9 ± 1.7	26.0 ± 0.4
30.0	0.1108 ± 0.0051	1.1172 ± 0.0057	44.8 ± 4.1	16.3 ± 2.0	25.1 ± 0.4
32.5	0.1082 ± 0.0066	1.1143 ± 0.0073	19.0 ± 1.4	7.9 ± 0.9	19.1 ± 0.2
33.5	0.0108 ± 0.0089	1.0109 ± 0.0090	17.5 ± 3.1	1.2 ± 0.2	22.3 ± 1.1

^aThe values are given as Mean ± SE

Discussion

During the present study, temperature-dependent patterns of development of *B. rubrioculus* were precisely determined under constant temperatures. The survival and the time necessary for development were expectedly affected by temperature through all immature stages. These results indicated that brown mites could produce offspring in a wide range of temperatures.

Keshavarz Jamshidian *et al.* (2004) and Eghbalian *et al.* (2007) were investigated only biology of this mite on sour cherry at 22 and 25 °C, respectively. They reported that the development time of entire immature as 29.2 ± 0.5 and 36.2 ± 0.7 days at the mentioned temperatures. Also, Honarparvar *et al.* (2012) investigated the effect of nine temperature between 15 and 35 °C on sweet cherry and reported that *B. rubrioculus* was not able to complete life cycle at 35 °C. They used insufficient points to estimate the developmental rate by non-linear models, especially around the optimum and therefore could not estimate optimum and upper threshold temperatures. They found that the development time of entire immature was 43.4 ± 0.63 and 14.5 ± 0.37 days at 15 and 32.5 °C, respectively. Recently, Javadi Khederi and Khanjani (2014) studied effect of five constant temperatures between 20 and 32.5 °C on demographic parameters of *B. rubrioculus* on apple leaf discs. They observed that brown mite was not able to complete life cycle at 32.5 °C.

In the present study, the shortest adult longevity occurred at 33.5 °C suggests that females of *B. rubrioculus* are sensitive to temperatures more than 30 °C. Some other authors have indicated that 32.5 °C was much less favorable for oviposition than 30 °C (Honarparvar *et al.* 2012; Javadi Khederi and Khanjani 2014), because brown mites discontinued laying eggs at the higher temperatures, which partly confirms our data.

It is difficult to compare the effect of temperature on egg hatch and development time of entire immature stages recorded in this study with that reported by Herbert *et al.* (1962), because different temperatures were used. Moreover, Herbert (1962) successfully incubated eggs at 10 °C, possibly because of thermal adaptation of the Canadian population of *B. rubrioculus* to cold climate. The highest temperature that Herbert (1962) examined was as 18.3 °C, which all stages developed with varying degrees of survival.

Javadi Khederi *et al.* (2014) observed most eggs of brown mite didn't hatch at 17.5 and 32.5 °C, therefore the temperatures are not favorable for egg development whereas another similar study on sweet cherry confirm our result which it showed eggs were hatched in 15, 17.5 and 32.5 °C (Honarparvar *et al.* 2012). The effects induced by the different host plant on specific biological parameters of brown mite (*i.e.*, oviposition rate, cycle duration, longevity, etc.) could express differences in host acceptance and they should be investigated for a wider consideration of host resistance/susceptibility, extending the observations for more successive generations in order to take into account of possible physiological adaptations of the mite to the cultivars in the long-term period (McIntyre and Whitham 2003).

Numerous mathematical functions can describe developmental rate versus temperature curve. Many models used for modeling development rates, cannot predict acceptable results. Degree-day method is usually used for estimating physiological time that expresses the total number of degree-days needed to complete development. It has manifest advantages such as its simplicity and ease in estimating the thermal constant (Worner 1992). The Ikemoto and Takai's (2000) equation is new form of ordinary regression equation that estimates the lower temperature threshold and thermal constant more precisely. Moreover, the linear model does not provide the optimal temperature and

the upper temperature threshold. Honarparvar *et al.* (2012) suggested 4.9 °C and 400 day-degree as lower threshold temperature (t) and thermal constant (k). While Javadi Khederi and Khanjani (2014) were estimated these values as 12.9 °C and 279.7 degree-days (DD). In addition, we calculated a total of 361.3 degree-days above the threshold temperature (8.9 °C) were required to complete development from egg to adult which was lower than that 400 DD for *B. rubrioculus* on sweet cherry.

The non-linear models are more difficult to fit than linear models and considering that they require more preparation with the specification of the model and initial guesses for parameter values. Three models including Analytis1/Allahyari, Hilbert and Logan, and Logan-6 models were selected based on goodness of fit and biological significance. We used the AIC for obtain goodness of fit, which is parameter independent (Akaike 1974). Furthermore, the ability to estimate key points (*i.e.*, T_{min} , T_{opt} and T_{max}) is an extremely critical feature of such models. The Logan-6 model (Logan *et al.* 1976) described developmental rates at intermediate and high temperatures. Some models are unable to estimate the lower temperature threshold (Briere and Pracros 1998). We fitted Analytis1/ Allahyari model with development rates of total immature of *B. rubrioculus* and provided realistic values for T_{opt} and T_{max} , but development was not observed over several degrees above the estimated low temperature threshold. Overall, we found that Analytis1/ Allahyari, Hilbert and Logan, and Logan-6 models best modeled the developmental rate of entire immature stages of *B. rubrioculus* because they principally attempt to cover the curve for the entire temperature range within the developmental limits, and the parameters have biological meaning as well. In this regard, Javadi Khederi and Khanjani (2014) point out the critical temperatures (T_{min} , T_{opt} and T_{max}) for the same mite, using the non-linear models ranged from 6.6, 29.3 and 30.6 respectively. Obviously, here the lower thermal threshold, which was found by them, on the same mite, was partly similar to our findings although, the optimum and maximum developmental temperatures in our study was higher than that they observed.

The Weibull, model gave a satisfactory fit to our data over the temperature range tested, indicated by low values of SSE. It seems, however, that Weibull model tends to overestimate l_x close to the end of survival period. Therefore, they bracket the data to over and underestimate parameters. The data obtained by us, could not be fitted with Analytis model, but closer to the Weibull-fitted l_x , although, there are problems, which need to be discussed. Firstly because, the Weibull l_x has extended too much older age than the experimental data, and secondly, the Weibull function is a descending function, it gives always $l_{x+1} < l_x$. But we should consider that, the real survival curves are seldom a smooth descending curve and sometimes there are no mortalities during a specific period or stage. Although, in our study of sour cherry brown mite, we used Weibull- l_x indexed from age 0 (the egg stage), and not "adult" age, so, we could express, that, our results of fittings are more real than those based on adult age. Because the age-specific survival rate should not be fitted to an equation while ignoring the closely related age-specific fecundity as well as its effect on the population parameters, we suggest that the use of Weibull function model should be reconsidered. Acquisition of age-stage survival rates (s_{xj}), was an important achievement for our research, as it showed by us, the adults could emerge at different ages, and disproves as erroneous the possibility that the survival rate should be based on "female adult age". In our study, immature survival was the lowest at 15, 32.5 and 33.5 °C; therefore, the optimal range for immature survival seems to fall midpoint of this range.

The age specific fecundity (m_x) curves of *Bryobia rubrioculus* is indicated varies value on different temperatures which these curves revealed that the age specific fecundity schedule fluctuated throughout the oviposition period, showing an asymmetrical pattern, skewed toward older individual.

The life table parameters are a good tools for evaluate and understanding effects of temperature and host on the growth, survival, reproduction and increase rate of an insect (Bellows *et al.* 1992) and understanding of these values are important in integrated pest management. The intrinsic rate of increase (r) and fecundity have been used as indicators of the pest population performance and they are very important in relation to different pest population growth studies in particular in two-spotted spider mites (Sabelis 1985b). The parameter r integrates the effects of mortality and fecundity into a single value, therefore, it is crucially influenced by a wide range of variables including pre-imaginal survival, developmental rate, longevity of females, fecundity schedule and sex ratio, which are all affected by temperature. Highest values of r obtained at 30 °C (0.1108 day⁻¹) while total progeny per female had the highest values at 17.5 °C. Hence, a lower temperature of the r was frequently balanced by the additive value of another examined temperature. For example, at 32.5 °C, low pre-imaginal survival was offset by a short pre-imaginal development time, and low progeny production was offset by a short generation time. The available set of temperature-dependent life history variables influence differentially on the r -temperature relationship. At 30 and 32.5 °C, shorter life span of female appears as a major factor to rising r .

In this survey, we showed pattern for reproductive response to constant temperatures. Using data of demographic parameters, we compared the potential of brown mite for population growth under various temperatures. *B. rubrioculus* is enable to develop the highest populations at 30 °C temperature. Shorter development and faster reproduction of *B. rubrioculus* at 30 °C lead to higher performance than other temperatures. These reasons could partly explain the rapid increase of brown mite populations in sour cherry orchards during spring. We know that arthropods are subjected to complex conditions in their natural environment. In orchards, dynamic of mites may also be changed by natural enemies, plant growth and their own density. Hence, before implementing these results to predictive population dynamics, further physiological and ecological studies are warranted to quantify the rate of population growth and development under fluctuating temperatures. Knowledge of these parameters can provide a starting point for developing a model that could be applied to brown mite population growth. In addition, this study can be used for future studies on efficiently managing the sour cherry orchards.

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دموگرافی کنه قهوه‌ای پابلند *Bryobia rubrioculus* (Acari: Tetranychidae) پرورش داده شده روی برگ‌های آلبالو در دماهای ثابت

محمد علی سلیمانی*، محمد خانجانی، بابک ظهیری و سعید جوادی خدری

گروه گیاه‌پزشکی، دانشکده کشاورزی، دانشگاه بوعلی سینا، همدان؛ رایانامه‌ها: soleimani.m.a@gmail.com، mkhanjani@gmail.com، Javadis84@gmail.com، bzahiri@basu.ac.ir

* نویسنده مسئول

چکیده

چرخه زیستی کنه قهوه‌ای پابلند روی برگ درخت آلبالو در دماهای ۱۵، ۱۷/۵، ۲۰، ۲۲/۵، ۲۵، ۲۷/۵، ۳۰، ۳۲/۵ و ۳۳/۵ درجه سلسیوس، رطوبت نسبی 65 ± 5 درصد و دوره نوری ۱۶ ساعت روشنایی و ۸ ساعت تاریکی مطالعه شد. طولانی‌ترین و کوتاه‌ترین مجموع دوره رشد و نمو مراحل نابالغ کنه قهوه‌ای در دماهای ۱۵ و ۳۲/۵ درجه سلسیوس به ترتیب $62/6 \pm 1/66$ و $14/2 \pm 0/20$ روز بود. با افزایش دما از ۱۵ به ۳۲/۵ درجه سلسیوس، طول عمر کنه‌ها از $83/5 \pm 2/14$ تا $24/7 \pm 0/39$ روز کاهش یافت. بیش‌ترین و کم‌ترین میزان بارآوری کل به ترتیب با $37/3 \pm 1/63$ و $6/3 \pm 1/06$ تخم در دماهای ۱۷/۵ و ۱۵ درجه سلسیوس مشاهده شد. بیشترین نرخ ذاتی رشد (r) در دمای ۳۰ درجه سلسیوس به دست آمد ($r = 0/1108 \pm 0/005$). میانگین طول یک نسل (T) در دماهای ۱۵ و ۳۲/۵ درجه سلسیوس به ترتیب $78/1 \pm 2/8$ و $19/1 \pm 0/2$ روز مشاهده شد. داده‌های مرتبط با زنده‌مانی ویژه سنی (l_x) با مدل ویبول برازش داده شد. آستانه دمایی پایین (t) و ثابت حرارتی (k) مراحل نابالغ با استفاده از مدل خطی ایکه‌موتو و تاکایی ۸/۹ درجه سلسیوس و $361/3$ روز-درجه تخمین زده شد. نرخ رشدی مراحل نابالغ با مدل‌های غیر خطی آنالیتیس-اللهیاری، هیلبرت و لوگان، و لوگان-۶ برازش داده شدند و دمای بهینه رشد با مدل‌های فوق به ترتیب ۳۳/۱، ۳۳/۹۰ و ۳۲/۴۰ درجه سلسیوس تخمین زده شد. واژگان کلیدی: جدول زندگی، دوره رشد و نمو، دما، ثابت حرارتی، پیش‌استیگمایان.

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